Towards the sustainable management of recreational fisheries: accounting for diversity in angler behaviour and fish life history

D i s s e r t a t i o n

zur Erlangung des akademischen Grades
(for the Completion of the Academic Degree)
"Doctor Rerum Agriculturarum"
(Dr. rer. agr.)

eingereicht an der
Landwirtschaftlich-Gärtnerischen Fakultät
der Humboldt-Universität zu Berlin
(submitted to the
Faculty of Agriculture and Horticulture
at Humboldt-Universität zu Berlin)

von
M.Sc., Fiona Dawn Johnston

Präsident der (President of the)
Humboldt-Universität zu Berlin:

Prof. Dr. Jan-Hendrik Olbertz

Dekan der Landwirtschaftlich-Gärtnerischen Fakultät:
(Dean of the Faculty of Agriculture and Horticulture)

Prof. Dr. Dr. h.c. Frank Ellmer

Gutacher/in (Reviewers): 1. Prof. Dr. Robert Arlinghaus

2. Dr. Michael S. Allen

3. PD Dr. Thomas Mehner

Eingereicht am (Submitted on): 5 März 2014

Tag der mündlichen Prüfung (Date of Oral Exam): 1 Juli 2014

TABLE OF CONTENTS

LIST OF PAPERS

I. Johnston, F.D., R. Arlinghaus, J. Stelfox, and J. R. Post. 2011. Decline in angler use despite increased catch rates: anglers' response to the implementation of a total catch-and-release regulation. Fisheries Research. 110(1): 189-197.

II. Johnston, F. D., R. Arlinghaus, and U. Dieckmann. 2010. Diversity and complexity of angler behaviour drive socially optimal input and output regulations in a bioeconomic recreational-fisheries model. Canadian Journal of Fisheries and Aquatic Sciences 67(9): 1507-1531.

Johnston, F. D., R. Arlinghaus, and U. Dieckmann. 2010. Erratum: Diversity and complexity of angler behaviour drive socially optimal input and output regulations in a bioeconomic recreational-fisheries model. Canadian Journal of Fisheries and Aquatic Sciences 67(11), 1897-1898.

III. Johnston, F. D., R. Arlinghaus, and U. Dieckmann. 2013. Fish life history, angler behaviour and optimal management of recreational fisheries. Fish and Fisheries 14(4): 554-579.

IV. Johnston, F. D., B. Beardmore, and R. Arlinghaus *Submitted*. Optimal management of diverse recreational fisheries in the presence of hooking mortality and noncompliance. Canadian Journal of Fisheries and Aquatic Sciences

(Revised manuscript now published: Johnston, F. D., Beardmore, B., and Arlinghaus, R., 2015. Optimal management of recreational fisheries in the presence of hooking mortality and noncompliance — predictions from a bioeconomic model incorporating a mechanistic model of angler behavior. Canadian Journal of Fisheries and Aquatic Sciences 72(1):37–53)

V. Gwinn, D. C., M. S. Allen, F. D. Johnston, P. Brown, C. R. Todd, and R. Arlinghaus. *In Press*. Rethinking length-based fisheries regulations: the value of protecting old and large fish with harvest slots. Fish and Fisheries. DOI: 10.1111/faf.12053.

ABSTRACT (ENGLISH)

Recreational fisheries are complex social-ecological systems, and managers often need to balance the interests of the anglers utilizing the fishery – the social sustainability – and the biological sustainability of the fish population. However, a poor understanding of the interactions among the main components of a fishery – the biological, social, and management components – has limited our ability to manage recreational fisheries sustainably. Fish life-history type (LHT), the dynamics and diversity of the angler population, angling regulations and management objectives all influence management outcomes. Using both empirical and theoretical studies, I evaluated the importance of jointly considering these primary drivers and the feedbacks between fishery components when managing recreational fisheries. I developed a novel bioeconomic modelling framework to determine which regulations (effort regulations and minimum-size limits) maximized the social welfare derived from the fishery, the optimal social yield (OSY). My research refutes the hypothesis that anglers are self-regulating (i.e., stop fishing when catch rates decline). The amount and type of fishing pressure the fishery received and the social welfare derived were strongly influenced by multiple fishery attributes and differed with the type of angler fishing and the fish population's vulnerability to overexploitation (LHT). I found regulations influenced fishing mortality rates, but also directly influenced angler behaviour. Some regulations were more effective than others at achieving management objectives, but their effectiveness could be undermined by hooking mortality and regulatory noncompliance. Despite differences in optimal regulations, an OSY management approach generally did not result in overfishing. My research demonstrates that a multidisciplinary approach based on clear objectives can help us progress towards both socially and biologically sustainable management of recreational fisheries.

ZUSAMMENFASSUNG (DEUTSCH)

Die Freizeit- bzw. Angelfischerei ist ein komplexes sozial-ökologisches System, welches sich aus drei wesentlichen Komponenten zusammensetzt: einer biologischen, einer sozialen und einer Managementkomponente. Fischereimanager sind aufgefordert, anglerischen Interessen und den Anforderungen einer biologisch nachhaltigen Gewässerbewirtschaftung gleichsam gerecht zu werden. Unzureichend verstandene Wechselwirkungen zwischen den Fischereikomponenten limitieren die Möglichkeit, die Angelfischerei nachhaltig zu entwickeln. Diese werden beeinflusst von lebensgeschichtlichen Parametern der jeweiligen Fischart, von Dynamik und Diversität der Angler sowie von Maßnahmen und Managementzielen. Die Dissertation untersuchte die Bedeutung einer gleichzeitigen Berücksichtigung der drei Fischereikomponenten und ihren Wechselwirkungen zur Realisierung einer biologisch und sozial nachhaltigen Angelfischerei. Ein neuartiges bioökonomisches Simulationsmodell identifizierte Bewirtschaftungsmaßnahmen, die den von der Fischerei erzeugten sozialen Nutzen maximieren. Die Ergebnisse widerlegen die Annahme der Selbstregulationsfähigkeit der Angelfischerei. Die Höhe und Art der Befischungsintensität sowie der soziale Nutzen wurden stark durch eine Vielzahl von fangabhängigen und fangunabhängigen Attributen beeinflusst, wobei auch Anglertyp und Anfälligkeit der Fischpopulation zur Überfischung eine Rolle spielten. Einige Regularien zur Erreichung der Bewirtschaftungsziele waren effektiver als andere, aber ihre Wirksamkeit könnte durch die Haksterblichkeit und die Nichteinhaltung von Vorschriften unterlaufen werden. Obwohl sich die Bewirtschaftungsmaßnahmen je nach Zielart, Anglerschaft und Bewirtschaftungszielen richten, beinhalten die als optimal identifizierten Maßnahmen in fast allen Fällen eine biologische nachhaltige Bewirtschaftung. Die Ergebnisse zeigen, dass ein interdisziplinärer Ansatz zu einer sozial und biologisch nachhaltigen Bewirtschaftung der Freizeitfischerei beitragen kann.

1 BACKGROUND

In the temperate, developed world, recreational fishing is the dominant use of many marine and most inland fish stocks (Arlinghaus et al. 2002), with participants comprising 10% to as high as 50% of the adult population in some countries (Arlinghaus and Cooke 2009). Ignoring the non-market value of these resources, the economic revenue generated by recreational fisheries may be comparable or greater than that generated by commercial fisheries (Post et al. 2002). Yet, recreational fishing is often perceived to be relatively benign (McPhee et al. 2002, Cooke and Cowx 2006), because catchability (the efficiency with which fish are captured) is often considered to be low (Cox and Walters 2002, Cooke and Cowx 2006), and because it is often assumed that anglers are self-regulating (i.e., abandon fisheries when they become depleted) (Cox and Walters 2002, Post et al. 2002, Radomski 2003). Thus, the impacts of recreational fishing on fish populations are often ignored (McPhee et al. 2002, Cooke and Cowx 2006), or go unnoticed due to insufficient monitoring (Post et al. 2002). However, recreational fishing effort and harvest can be high (McPhee et al. 2002, Coleman et al. 2004, Cooke and Cowx 2004, 2006), with annual exploitation rates as high as 80% being reported in some systems (Lewin et al. 2006). Recreational fishers may also be allowed to target vulnerable populations or life stages that commercial fishers are restricted from utilizing (Coleman et al. 2004, Cooke and Cowx 2004), and, due to the complexity of angler behaviour, may not behave in a self-regulating manner (Post et al. 2002, Beard et al. 2003). Thus, recreational fisheries can be an important contributor to the decline of global fish populations (McPhee et al. 2002, Post et al. 2002, Coleman et al. 2004, Cooke and Cowx 2004, 2006).

Sustainable Management

Managers are faced with the challenge of balancing the interests of angling groups – the social sustainability – with concerns about the biological sustainability of exploited fish populations (Radomski et al. 2001, Peterson and Evans 2003). The impacts of fishing on fish populations include demographic changes through truncation of the natural age and size structure (Hutchings and Reynolds 2004, Lewin et al. 2006), the release from interspecific competition which may result in phenotypically plastic changes in life-history traits such as growth and maturation (Lorenzen and Enberg 2002, Lewin et al. 2006), and, if fishing acts as a selective force, evolutionary changes in life-history traits (Heino and Godø 2002, Lewin et al. 2006, Allendorf and Hard 2009). Management actions will alter these impacts by

influencing the amount and type of fish that can be legally harvested and the amount and type of fishing pressure the fishery receives. However, recreational fisheries are social-ecological systems. Any changes to the biological component of the fishery, and indeed in the regulations themselves, will have consequences for the perceived quality of the fishery by the angler community and the corresponding social welfare (alternatively termed benefits, satisfaction, or utility) derived from the fishery. Thus, when managing recreational fisheries, managers must be concerned with both the biological and social sustainability of the fishery.

1.1 Biologically Sustainable Management

In terms of the biological sustainability of a recreational fishery, the success of any management action will depend on: (*i*) the intrinsic vulnerability of the fish population to overexploitation, which is influenced by the fish life history, (*ii*) the ability to accurately predict fishing effort, which is influenced by the type of angler fishing and their associated behaviour, and (*iii*) how effective management actions are at controlling the negative impacts of fishing, which is influenced by the type of regulations used and their effectiveness. The drastic decline or collapse of some recreational fish populations (McPhee et al. 2002, Post et al. 2002) suggests that management strategies have not always been successful.

1.1.1 Fish life history

The impacts of angling on recreational fish populations, both in terms of population declines and changes in the demographic structure, depend on the life history of the species being exploited. A species' life-history traits (describing, e.g., growth, maturation, or fecundity) will influence its intrinsic vulnerability to overexploitation, because, in combination, they determine the timing and magnitude of reproduction and mortality (Stearns 1992). Life-history traits vary substantially among species and populations (Stearns 1992, Reynolds et al. 2001) and are often phenotypically plastic (Pigliucci 2005). The combination of life-history traits, i.e., a species' life-history strategy, is the evolutionary outcome of natural selection that maximizes lifetime reproductive success under the constraints imposed by trade-offs between time and how energy is allocated among such things as growth, reproduction, and somatic maintenance (Stearns 1992, Reynolds 2003). The "fast-slow continuum" is often used to describe the range of potential life-history strategies, with "fast" applying to species that mature early and produce large numbers of offspring, and "slow" applying to those that delay maturation, attain a larger body size and produce fewer larger offspring over extended periods (i.e., have low potential rates of population increase) (Reynolds 2003). Fish that

exhibit different life-history strategies differ in their productivity, and thus in the amount of fishing mortality they can sustain (Reynolds et al. 2001). Furthermore, the degree to which density-dependent processes regulate populations differs, altering their ability to compensate for fishing mortality (Rose et al. 2001, Winemiller 2005, Goodwin et al. 2006). For example, fish with slower life histories have been reported to be more vulnerable to overexploitation than fish with the opposite characteristics (Jennings et al. 1998, Reynolds et al. 2001). This suggests that the large-bodied predatory fish with slower life histories commonly targeted by recreational anglers in many countries (Arlinghaus et al. 2002, Lewin et al. 2006), are at risk of overexploitation. However, in fish, the negative correlation between body size and extinction risk is equivocal (Duncan and Lockwood 2001, Reynolds et al. 2005, Pinsky et al. 2011, Hutchings et al. 2012). Thus, to predict how fish populations will respond to exploitation, quantitative modelling approaches that account for differences in life-history traits are required (Rose et al. 2001).

1.1.2 Angler dynamics and heterogeneity

The impacts of angling on recreational fish populations also depend on the amount and type of fishing pressure the fishery receives. Past research on sustainable fisheries management has generally only considered the ecological component of recreational fisheries – the dynamics of the fish population. The social component – the dynamics of the angler population – has been largely disregarded (Hilborn and Walters 1992, Johnson and Carpenter 1994, Aas and Ditton 1998, Radomski et al. 2001, Cox and Walters 2002, Beard et al. 2003, Metcalf et al. 2010). Yet, ignoring angler dynamics introduces large implementation uncertainty to any management action (Fulton et al. 2011), as the amount of fishing effort a fishery receives will strongly influence the impacts that fishing has. Thus, for management actions to be effective, an understanding of not only how fish respond to exploitation, but also how anglers alter their fishing behaviour in response to social and ecological changes in the fishery is required (Radomski et al. 2001). Consequently, the behavioural dynamics of anglers must be incorporated into integrated fisheries-management models (Johnson and Carpenter 1994, Radomski et al. 2001, Post et al. 2008, Fulton et al. 2011, Fenichel et al. 2013a, Post 2013).

When angler-effort dynamics are considered, studies generally assume them to be predominantly or exclusively driven by catch rates or by some other measure of fish abundance (e.g., Johnson and Carpenter 1994, Beard et al. 2003, Post et al. 2003). However,

unlike commercial fisheries in which fishers attempt to maximize profit or employment (Hilborn 2007), maximizing harvested biomass may not be the primary factor determining anglers' fishing decisions (Post et al. 2002, Cox et al. 2003). Behaviour of recreational anglers is likely much more complex, and thus harder to predict (Fenichel et al. 2013a). It is known from human dimensions research on recreational fisheries that multiple attributes of the fishery system drive anglers' behavioural decisions (Hunt 2005). Availability of preferred species, catch rates, fish size, congestion, facilities available, distance, and angling regulations are some of the attributes that are thought to affect anglers' participation decisions (Hunt 2005). In ecological terms, such complex multi-attribute-based behaviour produces a disconnect between the predator and its prey because the number of predators is not constrained by the number of prey (Johnson and Carpenter 1994). This makes it difficult to quantify the numerical response of anglers (Post et al. 2002), and thus the impact they will have on the fish population.

A further consideration is that it is unlikely that all anglers behave the same. Rather, it is more likely that the angler community is made up of a mixture of diverse angler types who are heterogeneous in their fishing preferences. The relative importance of fishery attributes, and thus the utility (satisfaction) they derive from fishing, varies among angler types (Jacobson 1996, Aas et al. 2000, Hunt 2005, Oh et al. 2005a, Oh and Ditton 2006, Beardmore et al. 2011). Hence, the participation decisions of angler types differ, because their perceptions of fishery quality are not the same. Furthermore, various types of anglers may also differ in their fishing practices – for example, they may have different skill levels, target fish of different sizes, utilize different gear, and differ in their propensity to voluntarily release fish (Bryan 1977, Hahn 1991, Fenichel et al. 2013a, Heermann et al. 2013, Ward et al. 2013). Based on recreation specialization theory it has been suggests that there is a continuum in angler behaviour from the least specialized anglers, that are casually involved, to the most specialized, that are setting and technique specialists (Bryan 1977, Ditton et al. 1992). It is thought that as specialization increases, so does commitment to angling, skill level, and the importance of fish size, (Bryan 1977, Hahn 1991), while the importance of harvesting fish declines (Oh and Ditton 2006, Arlinghaus 2007). Given such diversity, the impact that recreational fishing has on fish populations likely varies with the composition of the angler population (Dorow et al. 2010, Fenichel et al. 2013a).

1.1.3 Management options and regulation efficacy

The impacts of angling on recreational fish populations also depend on the amount of mortality anglers can impose on the fishery. Harvest regulations are tools commonly used in recreational fisheries to minimize the negative impacts of fishing (Radomski et al. 2001, Allen et al. 2013), particularly in open-access fisheries that pervade in North America (Cox and Walters 2002, Post 2013). These output regulations include, for example, daily harvest limits (i.e., bag limits, creel limits) or size-based harvest regulations such as minimum-size limits. However, in less productive fisheries few anglers actually catch their limit (Baccante 1995, Cook et al. 2001), and consequently daily harvest limits may be ineffective (e.g., van Poorten et al. 2013). Minimum-size limits (MSLs) are the most commonly used size-based regulations (Radomski et al. 2001), but can result in the truncation of the size- and age-structure of the fish population (Lewin et al. 2006, Arlinghaus et al. 2010). The loss of large, and hence more fecund, fish from the population can erode compensatory capacity (Birkeland and Dayton 2005, Lorenzen 2008, Arlinghaus et al. 2010), and impair long-term biological sustainability of populations (Berkeley et al. 2004, Anderson et al. 2008, Hsieh et al. 2010). Thus, it is perhaps not surprising that MSLs have been reported to be ineffective at achieving management objectives such as increasing the proportion of large fish in the population and increasing overall fish abundance (Wilde 1997, Arlinghaus et al. 2010). Other, less commonly implemented, length-based regulations such as protected-slot limits, that protect intermediate size classes, or harvest-slot limits (HSLs), that protect large and small individuals, but allow the harvest of intermediate-sized fish, may be more effective for achieving such management objectives (Wilde 1997, Arlinghaus et al. 2010, Pierce 2010).

Output control measures are only effective, however, if released fish survive and successfully reproduce (Arlinghaus et al. 2007). The effectiveness of harvest regulations can be undermined by hidden sources of mortality, such as hooking mortality (death from handling or injury during the process of catch-and-release, also termed discard mortality) (Coggins et al. 2007, Pine et al. 2008) and noncompliance with regulations (Gigliotti and Taylor 1990, Caroffino 2013), either from deliberate illegal harvest or due to measurement error or lack of regulation awareness (Page et al. 2004, Page and Radomski 2006). While under the right conditions the percent of released fish dying from hooking mortality approaches zero, under less favourable conditions estimates as high as 90% have been reported (Hühn and Arlinghaus 2011). Similarly, regulatory noncompliance with bag limits may be low (e.g., 7%; Wilberg 2009), but with length-based harvest regulations values as high as 65% have been

reported (Pierce and Tomcko 1998, Sullivan 2002). Furthermore, noncompliance can be a depensatory process (Allee effect) where the per capita mortality probability increases as catch rates, and underlying populations, decline (Sullivan 2002, Näslund et al. 2010). Post et al. (2002) and Post (2013) have warned that noncompliance may be an important component contributing to the collapse of recreational fisheries. Thus, accounting for both hooking mortality and noncompliance is important for ensuring the sustainability of recreational fisheries, yet few models do so explicitly.

It must also be recognized that output regulations, such as the ones previously mentioned, apply to individual anglers. They do not limit the number of anglers fishing and thus not the total harvest/mortality that the fishery experiences (Radomski et al. 2001, Cox and Walters 2002, Cox et al. 2002). Therefore, even under very restrictive output regulations, overexploitation may still occur if angling effort is sufficiently high (Cox and Walters 2002, Cox et al. 2002, Post 2013). Indeed, depending on the life-history characteristics of the species being exploited, even the most restrictive regulations (e.g., zero harvest) will be ineffective if fishing effort and hooking mortality (Paul et al. 2003, Post et al. 2003, Coggins et al. 2007) or regulatory noncompliance (Gigliotti and Taylor 1990) are sufficiently high. Furthermore, increasing trends in the practice of voluntary catch and release (the voluntary release of legally harvestable fish) limit the ability of harvest regulations to alter the impacts of fishing (Allen et al. 2008, Ferter et al. 2013). To address such problems, input regulations that limit fishing effort, such as limiting the number of angling licenses issued or seasonal closures, may be used to limit the negative impacts of fishing (Cox et al. 2002). However, such management strategies are often controversial, particularly in areas where anglers have historically had open access to public waters (Cox and Walters 2002).

Regardless of the regulations used, management actions are not external to the dynamics of the fishery system. Regulations influence catch-related attributes, such as the type and number of fish caught and harvested, which in turn alter the utility that anglers derive from a fishing experience. Thus, regulations indirectly alter angler behaviour. Yet, anglers also respond directly to the regulations themselves (Beard et al. 2003). For example, some regulations may be perceived as overly restrictive (Aas et al. 2000, Oh et al. 2005b, Carlin et al. 2012), or as an indicator of stock status (Beard et al. 2003), leading to changes in anglers' fishing decisions. Thus, management regulations will affect the fish population, the angler population, and the interplay between them (Homans and Ruliffson 1999). Not accounting for these dynamics may lead to unanticipated responses to management actions, which have

implications for the sustainable management of recreational fisheries (Metcalf et al. 2010, Fulton et al. 2011, Fenichel et al. 2013a).

1.2 Socially sustainable management

In terms of the social sustainability of a recreational fishery, the success of any management action will depend on the amount of social welfare (alternatively termed benefits or utility) that the fishery generates, requiring a paradigm shift from traditional management approaches that focus on maximizing catch rates or yield. Past management strategies, such as a maximum sustainable yield (MSY) approach, do not incorporate the social benefits provided by a fishery that are not measured by yield alone (Bennett et al. 1978, Malvestuto and Hudgins 1996, Radomski et al. 2001, Fenichel et al. 2013a). Yet, there is no reason to assume that maximization of social welfare will occur when fishery yield is maximized (Cox et al. 2003). As an alternative, optimum social yield (OSY), is a management approach that integrates the social and economic aspects of a fishery with the biological aspects allowing for a management objective that maximizes the social welfare that a fishery provides to society (Roedel 1975, Malvestuto and Hudgins 1996). Thus, this approach is much better suited to recreational fisheries, because it incorporates numerous factors beyond catch or yield alone. Furthermore, OSY provides a single, unambiguous management objective which is needed to judge management successes (Bennett et al. 1978, Barber and Taylor 1990, Radomski et al. 2001, Irwin et al. 2011, Fenichel et al. 2013b). However, the OSY approach is rarely used in practice, possibly because of the difficulty of measuring the underlying quantities.

To progress towards socially sustainable management, it is necessary to quantify individual anglers' preferences for regulatory outcomes and the utility they derive (Fenichel et al. 2013b), something which will vary among diverse angler types (Aas et al. 2000, Oh et al. 2005a, Oh and Ditton 2006, Fenichel et al. 2013b). These diverse angler preferences, and resulting behavioural decisions, need to be integrated into recreational fisheries models designed to determine optimal management policies (Radomski and Goeman 1996, Arlinghaus et al. 2008), for example from an OSY perspective. Discrete choice models quantitatively describe angler preferences and predict angler behaviour (Fenichel et al. 2013a, Fenichel et al. 2013b), and are commonly used in recreational fishing demand studies (Fenichel et al. 2013a). Discrete choice models are based on random utility maximization theory (McFadden 1974), which assumes that anglers will choose the angling alternative that

maximizes their individual utility. The utilities of individual anglers then need to be weighted and aggregated using a social welfare function to provide a measure of social welfare that can be used to judge management outcomes (Perman et al. 2003, Fenichel et al. 2013b). Yet, few recreational fishing models based on utility theory have been developed to predict the optimal social welfare generated by different management schemes (e.g., Die et al. 1988, Jacobson 1996, Massey et al. 2006), and fewer still represent coupled social-ecological models that account for multi-attribute angler behaviour (e.g., Cole and Ward 1994, Homans and Ruliffson 1999, Woodward and Griffin 2003, Massey et al. 2006), and angler heterogeneity (e.g., McConnell and Sutinen 1979, Anderson 1993). Furthermore, how individual preferences should be weighted in a social welfare function will depend on the managers' objectives and their concerns about equity, thus, there is no consensus on how this should be done (Perman et al. 2003, Fenichel et al. 2013b). For example, the social welfare function designed to allocate resources in a way that maximizes the total utility of all users, would differ from one with the objective of equitably distributing resources among all users. Thus, management objectives will likely strongly influence the management regulations that are predicted to be socially optimal, and need to be explicitly stated *a priori* (Fenichel et al. 2013b).

1.3 Summary

In summary, three interrelated factors need to be jointly considered when managing recreational fisheries (Figure 1): (*i*) the social component which describes the heterogeneity and dynamics of fishers exploiting the fishery (Radomski et al. 2001, Wilen et al. 2002, Fulton et al. 2011, Fenichel et al. 2013a), (*ii*) the biological component which describes fish population dynamics given the life history of the species and its resulting intrinsic vulnerability to overexploitation (Reynolds et al. 2001, Rose et al. 2001, Winemiller 2005), and (*iii*) the management component which describes the influence of input and output regulations on the ecological and social dynamics of the fishery, and which evaluates the effectiveness of these regulations for achieving various biological and social management objectives (Radomski et al. 2001, Cox and Walters 2002, Beard et al. 2003). Only by integrating these three main components – social, biological, and management – into fisheries models can fisheries dynamics be understood and more robust management predictions achieved.

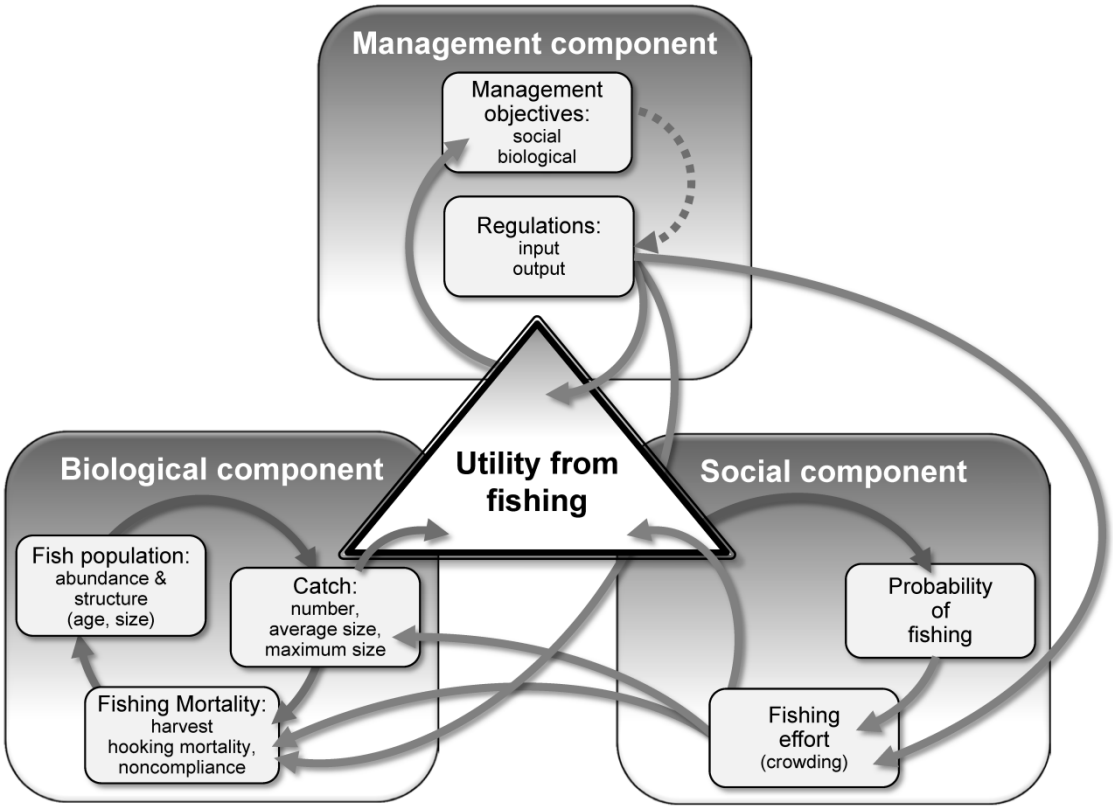


Figure 1. Schematic model of the main fishery components and their interactions.

2 RESEARCH OBJECTIVES AND STUDY QUESTIONS

The objective of my doctoral research was to evaluate the importance of jointly considering the social, biological, and management components of recreational fisheries for their biologically and socially sustainable management. Specifically, the aim was to address the following questions:

NOTE: Bold roman numerals in parentheses identify the relevant paper from the list of papers. Numerous papers may be relevant to a single question (see conceptual outline in Figure 2).

SOCIAL COMPONENT:

- How does dynamic angler behaviour influence recreational fisheries and their management **(I, II, III, IV)**?
- How does the consideration of multi-attribute angler behaviour impact sustainable fisheries management **(I, II, III, IV)**?

- How does angler heterogeneity in behavioural preferences influence recreational fisheries management **(I, II, III, IV)**?

BIOLOGICAL COMPONENT:

- Do different fish life-history types differ in their intrinsic vulnerability to over-exploitation **(III, IV)**?
- How does fish life history influence fish-angler dynamics **(III, IV)**?
- How does fish life history alter predictions about optimal management **(III, IV, V)**?

MANAGEMENT COMPONENT:

- How do hooking mortality and depensatory noncompliance influence the efficacy of management regulations **(IV, V)**?
- How does the use of harvest-slot limits (harvest of intermediate size classes) improve the efficacy of regulations in terms of achieving multiple management objectives, compared to the use of minimum-size limits **(V)**?
- How do predictions about optimal management change with differing management objectives **(II, V)**?

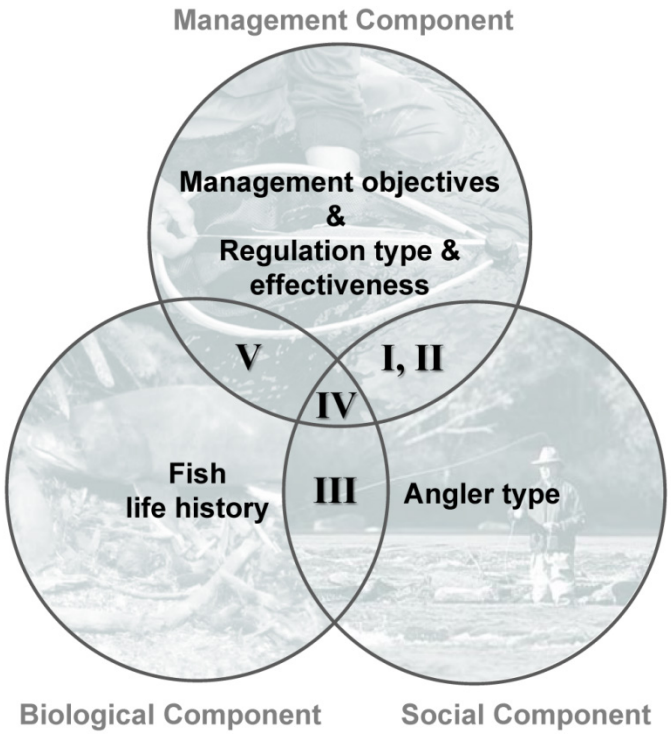


Figure 2. Conceptual outline of thesis papers in the context of fishery components and factors that affect them

3 METHODS SUMMARY

To address my research questions, I used both empirical (**I**) and theoretical approaches (**II**, **III**, **IV** & **V**).

3.1 Empirical methods

Paper I in my thesis examined the importance of considering the dynamic response of anglers to regulation changes, and their multi-attribute behaviour for recreational fisheries management. Population data from a recreationally-exploited char population (bull trout, *Salvelinus confluentus*), and two years of data from roving creel surveys of winter ice-anglers were used. The first year, 1992, represents conditions just prior to the implementation of a zero-harvest (total catch-and-release) regulation and organic bait ban. At this point in time, the bull trout population was heavily overexploited. The second year, 2002, represents conditions ten years after the regulation changes were implemented, at which point the fish population had rebuilt. Angler effort and catch-related attributes of the fishery – catch rates and the size structure of fish caught – were compared to determine if differences existed between before and after the bull trout population rebuilt, and if angler effort was positively related to catch quality. Voluntary catch information reported by anglers during the summer months from 1996 to 2003 was used to evaluate temporal trends and the correlation between the rebuilding of the fish population and catch-related attributes of the fishery.

3.2 Theoretical models

An integrated modelling approach, like the one depicted in Figure 1, that incorporates fish diversity, angler diversity, management actions, and their interactions is required to move towards the sustainable management of recreational fisheries. To this end, I developed an integrated bioeconomic model framework that involved linking an age-structured population submodel for a single-species, single-lake fishery (see details below), with a dynamic angler-effort submodel (see details below). Both input and output regulations, in the form of MSLs and license numbers, were the management tools considered. In summary, the age- and size-structure of the fish population, which was dependent upon the life-history type (LHT) of the fish, and the amount and type(s) of fishing effort (angler type), in combination, influenced the number and type of fish caught. The number and type of fish dying from fishing was dependent upon the structure of the catch, the harvest preferences (i.e., the propensity to voluntarily release fish) of the angler type(s) fishing, the MSL in place, and the presence and

magnitude of hooking mortality and regulatory noncompliance. The structure of the catch, in combination with direct preferences of angler types for angling regulations, influenced the utility that a given angler type derived from fishing, and thus the probability of that angler type choosing to fish. The probability of an individual angler fishing, in combination with the number of licenses issued and assumed maximum annual fishing effort, determined the annual fishing effort, which was calculated at the beginning of the year based on the previous year's experiences. Assessment of regulatory success was based on a socially optimal management objective (OSY), maximization of the social welfare (an aggregation of individual angler utilities) derived from the fishery. While there was no dynamic feedback between the welfare derived and the regulations implemented, one can imagine that this would be the next step if an adaptive management approach was to be taken. This model framework was used in **Papers II, III,** and **IV**.

3.2.1 Age-structured fish population submodel

In **Papers II, III** and **IV**, I used a deterministic, age-structured population to describe the dynamics of the fish population. To allow for the compensatory responses of the fish population to exploitation, I included two crucial density-dependent relationships: (i) density-dependent survival of the early life-stage (spawning to post-hatch), which is often included in fisheries models, and (ii) density-dependent growth in body size, which is much less commonly included (Lorenzen and Enberg 2002, Lorenzen 2008). To describe the selective nature of angling (Lewin et al. 2006), fishing mortality was assumed to be size-selective in two ways: (i) through the size-dependent vulnerability of fish to capture, where smaller individuals were less vulnerable to capture than larger ones, and (ii) through minimum-size limits, where harvest of fish below the regulated length was illegal. Fish reproduction was assumed to occur on an annual basis at the beginning of each year. However, fish mortality and the growth in body size of fish were described by continuous functions. This allowed our model to account for fish growth into vulnerable size classes and legally harvestable sizes within each year, and for the recapture and repeated exposure to hooking mortality of released individuals throughout the fishing season, both of which are important aspects of recreational fisheries (Coggins et al. 2007).

3.2.2 Dynamic angler-effort submodel

Economic theory assumes that if individuals are rational agents, they will make choices that maximize their personal utility (Perman et al. 2003). Based on such theory, it is assumed that

anglers have a higher probability of fishing when conditions provide them with more utility (Hunt 2005). Choice models based on random utility theory (McFadden 1974, Manski 1977), are statistical models that describe the relative contribution (the part-worth utility, PWU) of an attribute to an individual's utility, and make predictions about the probability of choosing an alternative from a selection of alternatives (Hunt 2005). This method has been used by human-dimensions researchers to predict how changes in a fishery affect angler use (e.g., Aas et al. 2000, Hunt 2005, Oh et al. 2005b, Oh and Ditton 2006). I used this approach to describe the angler-effort dynamics in my model. Such mechanistic models are more suitable that phenomenological models (e.g., Ideal free distribution models) for describing angler behaviour when obtaining measures of angler welfare and accounting for angler heterogeneity are important (Fenichel et al. 2013a).

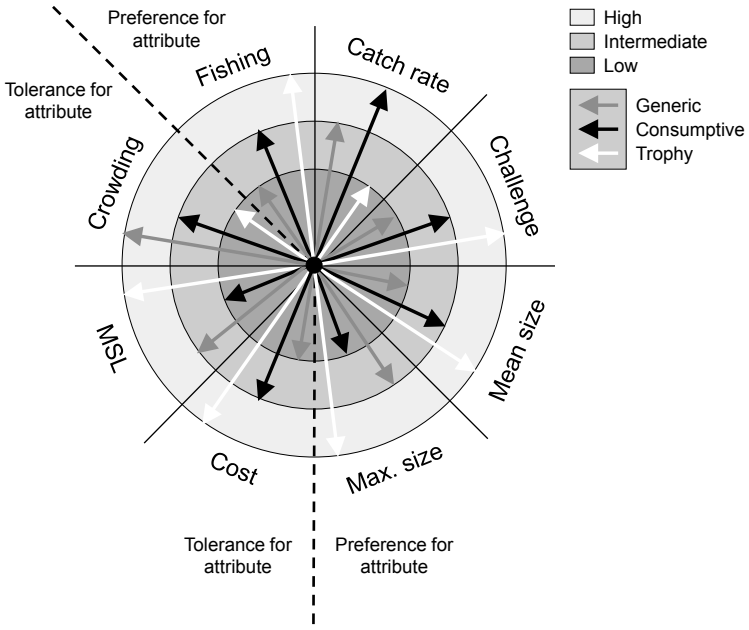


Figure 3. Qualitative differences in angler preferences for fishery attributes among the three different prototypical angler types (generic, consumptive, and trophy anglers). Gray circles indicate the relative preference levels or tolerance levels (low, intermediate, or high) of angler types for a particular fishery attribute. (Figure from **Paper II**)

In **Papers II** and **III**, behaviour of three prototypical angler types – generic, consumptive, and trophy anglers – was determined by angler-type-specific multi-attribute utility functions (Figure 3). These functions included the following fishery attributes: catch rates, average size of fish caught, maximum size of fish caught, angler congestion, minimum-size limit

regulations and license costs, all of which have been shown to affect anglers' fishing decisions (Hunt 2005). I developed these three stylized angler types based on angler specialization theory (Bryan 1977, Hahn 1991, Ditton et al. 1992, Fisher 1997). Thus, parameters for the utility functions, which described the fishing preferences of the different angler types, were chosen to reflect differential specialization, consumptive orientation, and overall dedication to the recreational fishing experience (see **Paper II** for detailed descriptions). Generic anglers were assumed to be the least specialized, consumptive anglers were intermediate, and trophy anglers were the most specialized, with consumptive anglers by definition having the greatest consumptive orientation and trophy anglers the least. I also assumed that they differed in their fishing preferences and fishing practices (e.g., skill/catchability, size of fish targeted, and propensity to voluntarily release fish). Figure 3 illustrates qualitatively how angler preferences for fishery attributes differed among the three prototypical angler types, and details are fully described in **Paper II**.

In **Paper IV**, I used an empirically based description of angler behaviour. Beardmore et al. (2013) carried out a stated-preference discrete choice experiment on anglers from the German federal state of Mecklenburg-Vorpommern. Using a latent class modelling analysis based on random utility theory (McFadden, 1974), Beardmore et al. (2013) found that, based on their preference diversity, anglers could be allocated to three classes (angler types), committed, casual and trophy anglers, comprising 58%, 33% and 9% of the sample, respectively. In addition to the fishery attributes described above, distance and bag limits were included in the experimental design by Beardmore et al. (2013). Based on this research, I calibrated the parameters for the PWU functions to describe the preferences of the three angler types used in **Paper IV**. Details of this process can be found in **Paper IV**.

3.2.3 Outline of analyses used in theoretical studies

Paper II examined the importance of considering the dynamic response of anglers to regulation changes, multi-attribute angler behaviour, and angler heterogeneity for socially optimal management. The biological component of the model was parameterized to describe a prototypical northern pike (*Esox lucius*) population, which is a popular target species in recreational fisheries in both North America and Eurasia (Paukert et al. 2001, Beardmore et al. 2011). To determine the importance of considering dynamic and complex angler behaviour, I altered the assumptions underlying the social component of the model by assuming: (*i*) that angler behaviour was static (fixed), (*ii*) that angler behaviour was

determined by catch rates alone, and (*iii*) that angler behaviour was complex, determined by multiple attributes of the fishery. Equilibrium outcomes were compared to determine how optimal regulations (minimum-size limits and license numbers that maximized aggregated total utility) differed among the three scenarios, and whether optimal regulations resulted in a biologically sustainable fishery. Biological sustainability was assessed using spawning-potential ratio (SPR); a metric which measures reductions in a fish population's reproductive output, and which has been used in recreational fisheries models as an indicator of recruitment overfishing (e.g., Coggins et al. 2007, Allen et al. 2009, Allen et al. 2013). To examine the influence of angler heterogeneity, all scenarios were simulated with angler populations composed solely of one of the angler types, and with an angler population that was made up of a mixture of angler types (40%, 30%, and 30% of generic, consumptive and trophy angler types, respectively). A further analysis was carried out in which I varied the welfare measure that determined optimal regulations to reflect differing management objectives. To do this I varied how the utility gained from fishing by the different angler types in a mixed angler population was weighted when the utilities were aggregated to obtain a measure of social welfare. This allowed us to assess how predictions about socially optimal regulations varied with differing management objectives (e.g., if managers were concerned with a more equitable distribution of resources or simply utility maximization).

Paper III examined how fish life history influenced fish-angler dynamics and predictions about the socially optimal of recreational fisheries. The biological component of the model was parameterized to describe five prototypical species; northern pike (*Esox lucius*), European perch (*Perca fluviatilis*), pikeperch (*Sander lucioperca*), brown trout (*Salmo trutta*) and bull trout (*Salvelinus confluentus*). These life-history types (LHTs) were chosen because they represent the broad range of life-history characteristics (illustrated in Figure 4) (Wootton 1984) of species commonly targeted by freshwater recreational anglers (e.g., Post et al. 2002, Almodóvar and Nicola 2004, Beardmore et al. 2011). To determine how vulnerability to overexploitation differed among LHTs, I examined the response of the fish populations to a range of fishing effort levels, where angler behaviour was static and the angler type was consumptive. I then explored how angler behaviour and diversity influenced predictions about socially optimal regulations and the biological (i.e., SPR) and social (i.e., total utility and annual fishing effort) conditions under these regulations. In these analyses, angler behaviour was assumed to be complex (driven by a multi-attribute utility function). Simulations were run with angler populations composed solely of one of the angler types, and

with four mixed angler population scenarios where the relative composition of the three angler types differed (i.e., 40%, 30%, 30%; 70%, 15%, 15%; 15%, 70%, 15%; 15%, 15%, 70%; for generic, consumptive and trophy angler types, respectively). Socially optimal regulations and the biological and social conditions under optimal regulations were examined.

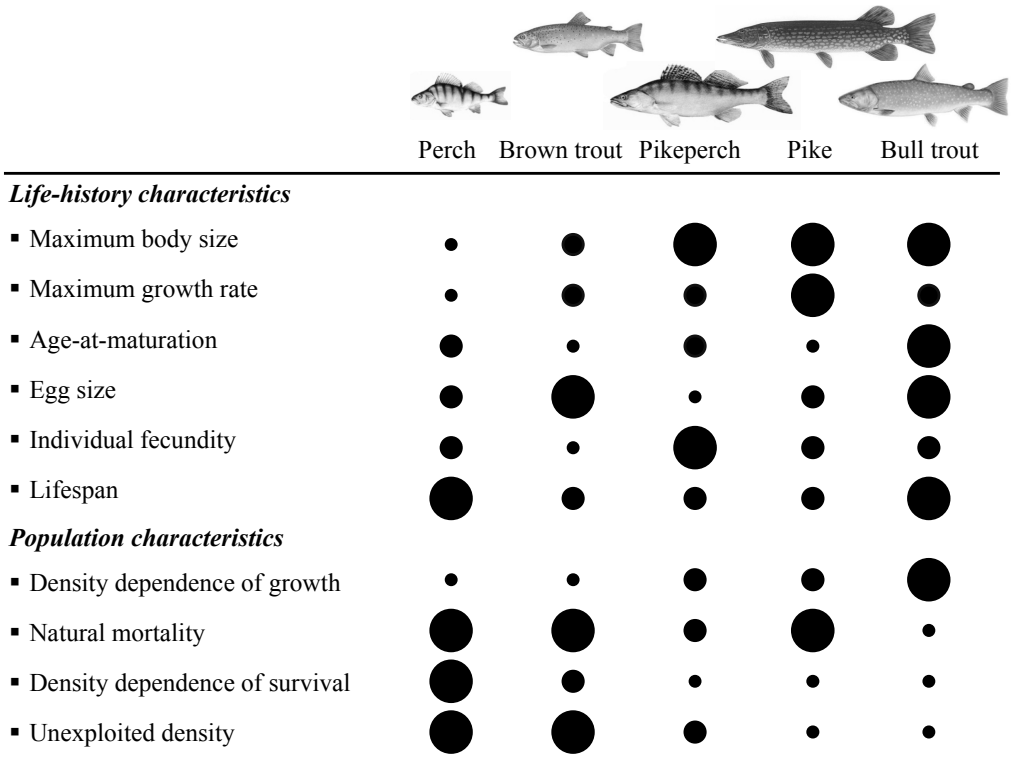


Figure 4. Qualitative description of variation in biological characteristics among the five considered fish life-history types. Small, medium and large circles represent low/small, intermediate and high/large levels, respectively. See **Paper III** for further details. (Figure from **Paper III**)

Paper IV examined how hidden sources of mortality, hooking mortality and regulatory noncompliance, influence the efficacy of management regulations. It expands on the work from **Papers II and III**, by incorporating empirically-based angler behaviour of the three diverse angler types reported by Beardmore et al. (2013), in addition to the five diverse fish LHTs used in **Paper III**. A recent review by Hühn and Arlinghaus (2011) on hooking mortality rates of European species important for recreational fisheries, or related species, found that the majority (57.1%) of hooking mortality estimates reported were under 10% (i.e., ≤ 10% of released fish died), and that estimates exceeding 50% mortality were rarely (7.9 %) reported. Reflecting this distribution, I considered five different levels of hooking

mortality, 0%, 5%, 10%, 25%, and 50%, in the presence and absence of regulatory noncompliance in **Paper IV**. Noncompliance with MSLs was modelled as a depensatory process, as has been reported by Sullivan (2002) and Näslund et al. (2010). I examined how hooking morality and regulatory noncompliance influenced regulation efficacy, in terms of averting recruitment overfishing, and how they influenced socially optimal regulations and the biological and social conditions under them. Finally, I examined the consequences of ignoring these hidden sources of mortality, and how hidden mortality affected management outcomes in open-access fisheries where effort regulations are not feasible.

Paper V compares the relative effectiveness of MSLs and harvest-slot limits (HSLs) for achieving diverse management objectives (i.e., maximizing harvest vs. maximizing trophy catch). The integrated modelling framework used in **Papers II, III and IV** was not used here. Instead, we used an age- and size-structured fish population model that incorporated numerous growth trajectories in order to more accurately represent the distribution of fish size within an age class that occurs in natural populations. Two generic prototypical fish LHTs, similar to those used by (Coggins et al. 2007), were modelled, in addition to six LHTs that represented recreational important fish species. For simplicity, fishing effort was represented by an instantaneous annual harvest rate, which was constant within a simulation, rather than having dynamic anglers. Intermediate and high exploitation rates were examined. We evaluated the model outcomes based on three management objectives, maximization of trophy catch, maximization of harvest, or a compromise objective where trophy catch and harvest were weighted similarly. The risk of recruitment overfishing and the truncation of the size distribution of the fish population were assessed under objective-meeting regulations. Results were compared between MSLs and HSLs.

4 MAIN FINDINGS AND DISCUSSION

4.1 The social component

Recreational fisheries are social-ecological systems. Unlike typical predator-prey systems, there is a disconnect between the numerical response of the predator to changes in prey abundance, because numerous factors both social and biological influence angler abundance (i.e., behaviour). A poor understanding of fish-angler dynamics has limited our ability to manage recreational fisheries in a sustainable manner. This has led to the recognition that not only the dynamics of the fish population need to be considered when managing these

fisheries, but also the dynamics of the angler community fishing and its response to management actions (Radomski et al. 2001, Fulton et al. 2011, Fenichel et al. 2013a, Post 2013). However, difficulties associated with the multidisciplinary nature of creating social-ecological models, have resulted in few studies undertaking this task (reviewed in Fenichel et al. 2013a). My approach of incorporating the primary drivers and feedbacks between the social, biological and management components of a recreational fishery (**Papers II, III & IV**) provides a solution for modelling this social-ecological system, bridging the gap between the fisheries and social sciences. In fact, Fenichel et al. (2013a) cites **Paper II** as one of the articles making a key contribution to this field of recreational fisheries modelling. In the following sections, I will discuss the importance of considering all three components of this social-ecological system for the biological and social sustainability of recreational fisheries management.

4.1.1 Biological sustainability

In terms of the biological sustainability of recreational fisheries, the bull trout population presented in **Paper I** was severely overexploited prior to the introduction of zero harvest regulations. Furthermore, **Paper I** clearly illustrates the disconnect between predator and prey populations. Counter to catch-based expectations, angler effort decreased, rather than increased, with the increasing catch rates and the increasing catch of trophy-sized fish that were experienced as the population recovered after the regulation change (**Paper I**). The findings from **Paper I**, in combination with information from other studies (e.g., McPhee et al. 2002, Post et al. 2002, Coleman et al. 2004, and review in Allen et al. 2013), refute the commonly held assumption that recreational anglers are self-regulating and, thus, leave the fishery when catch rates (which presumably correlate with fish population decline) drop (Cox and Walters 2002, Post et al. 2002, Post 2013). Implicit to the self-regulation hypothesis is the assumption that anglers behave dynamically, albeit solely in response to catch rates. Furthermore, this hypothesis assumes that anglers are highly responsive to catch rates, which, if not valid, can have dire consequences for the biological sustainability of a fishery (Allen et al. 2013). Despite this, for simplicity fishing effort is commonly assumed to be constant in fisheries models, or if angler dynamics are considered at all, it is assumed anglers respond solely to some metric that is related to catch rate, such as vulnerable population size (e.g., Post et al. 2003, Allen et al. 2013), progressing little beyond the assumption of self-regulation.

The absence of a positive relationship between increased catch rates and angler effort reported in **Paper I** supports suggestions that the assumption of catch-based self-regulation is overly simplistic (Post et al. 2002, Post et al. 2008), and demonstrates the need to better understand why anglers choose to fish where they do. Human dimensions researchers have found that multiple catch-related and non-catch-related attributes contribute to anglers' participation decisions (reviewed in Hunt 2005). Findings from **Paper II** suggest that not accounting for this complexity in angler behaviour can alter predictions about the amount of fishing effort that a fishery will attract, and the impacts that angling will have on the fish population. A key finding of **Papers II & III** was the theoretical prediction that anglers may continue to fish even when fish populations are depleted because of the appeal of other attributes of the fishery were able to compensate for the low utility derived from catch rates. This is a reasonable prediction given the overexploitation of some recreational fisheries (e.g., Post et al. 2002; **Paper I**). Thus, adopting a multi-attribute perspective on angler behaviour in recreational fisheries models will improve predictions about fishing effort and its consequences for the fish population.

My research (**Papers II, III & IV**) also indicates that is not only the complexity of angler behaviour, but also the diversity, i.e., the heterogeneity of the angling community, that is critical for predicting the impacts of angling on fish populations. It may be tempting to simplify model assumptions and use a description of average angler behaviour (Hahn 1991, Aas and Ditton 1998, Fenichel et al. 2013a). However, results from **Paper II** suggest that this would be in error, because the negative impact of angling on the fish population was generally greater when a mixed angler population was assumed. In terms of biological sustainability, **Papers II, III & IV** found that differences in both harvest practices (the propensity to voluntarily release fish) and angler preferences (e.g., the degree to which management measures inhibited behaviour, or the importance of other attributes over catch rate) played critical roles in predicting angler behaviour and the impacts fishing has on the fish population. Under various management scenarios, angler diversity results in changes in the composition of the anglers fishing, because of the differential responses of angler types to the management regulations themselves and the structure of the fish population the regulations produce (**Paper II**). An averaging approach to describing angler behaviour dilutes these differences and hence underestimates angling impacts (**Paper II**). Thus, my research indicates that current monitoring methods that pool information about anglers need to be modified. Instead, managers should obtain as much information as they can about the

composition of the angling community they are managing to effectively manage recreational fisheries.

A key point highlighted by my research, is that when predicting the biological impacts of fishing, it is important to remember that management regulations do not occur in isolation from the fish-angler system (Fenichel et al. 2013a). Harvest regulations may directly limit fish harvest by an individual angler, but they also affect angler behaviour (i.e., change fishing effort), which has indirect consequences for the biological sustainability of the fishery. In particular, harvest regulations may alter the attractiveness of a fishery if they are perceived to constrain anglers' opportunities to harvest fish (Radomski and Goeman 1996, Cox et al. 2002, Dorr et al. 2002), or if they alter anglers' expectations about fishery quality (Cook et al. 2001, Beard et al. 2003, Fayram et al. 2006). How regulations influence angler behaviour will vary with angler type (Beard et al. 2003), because how angler types perceive regulations will differ (e.g., Aas et al. 2000, Oh et al. 2005b). For example, Beard et al. (2003) found that walleye (*Sander vitreus*) anglers in general fished less on lakes with lower bag limits despite them having higher catch rates, whereas fishing effort by walleye-specific anglers did not differ across regulations. This finding agrees with my finding in **Paper I**, i.e., that angler effort decreased despite increases in catch-related aspects of the fishery and was likely due to a lack of tolerance by some anglers to restrictive harvest regulations. Yet, results from **Paper I** demonstrated that some anglers still fished, despite the total catch-and-release regulation, indicating that anglers were heterogeneous in their fishing preferences and behaviour.

One implication of angler responses to management actions is that they may alter or undermine the efficacy of regulations in terms of achieving management objectives (Radomski et al. 2001, Fayram and Schmalz 2006, Allen et al. 2013). For example, it is unknown if regulation changes would have been successful in rebuilding the bull trout population described in **Paper I** if angling effort did not decline. Even at moderate levels of fishing effort, low to moderate levels of hooking mortality or regulatory noncompliance can result in the overexploitation of bull trout (Post et al. 2003; Paper IV). Similarly, results from **Papers II & III** suggest that trophy anglers may have the greatest negative impacts on fish populations (in some cases overexploitation) under more restrictive regulations, because they continue to fish under restrictive regulations. This perhaps unexpected outcome would not have come to light if angler effort responses were not considered.

A potential area of future research, that I don't consider here, is the repercussions of management actions at the landscape scale. In open-access fisheries, improvements in fishery quality may be countered by an increase in angler effort, not only from the anglers already fishing the system but also from the attraction of new anglers to the fishery. Such increases in effort have the potential to reduce the quality once more, yielding a "success breeds failure pathology" (Cox and Walters 2002, Parkinson et al. 2004). Furthermore, displacement of anglers from one system (e.g., as occurred in LKL, **Paper I**) likely means that they will redistribute their effort within the angling landscape, having a spillover impacts on other systems (Lester et al. 2003). Thus, the sustainable management of recreational fisheries requires landscape-level considerations of angler dynamics (Post et al. 2008, Hunt et al. 2011, Post and Parkinson 2012).

4.1.2 Social sustainability

Who fishes and how much not only influences the biological impacts that anglers have on the fish population, but it also influences the welfare derived from the fishery and, thus, its social sustainability. **Paper II** demonstrates that management approaches designed to maximize catch result in suboptimal management (i.e., reduced utility), because of the numerous diverse attributes that contribute to angler utility (Hunt 2005). Furthermore, **Papers II, III & IV** show that regulations that maximize social welfare (optimal regulations) vary substantially with the composition of the angler community, demonstrating that the "who fishes" component (i.e., angler heterogeneity) is very important for the social sustainability of the fishery as well as its biological sustainability (see above). Certain management actions may lead to the under-representation, alienation, or exclusion of some angler types relative to others in mixed-angler fisheries, because of the differences in the relative attractiveness of the fishery conditions produced by the regulations to the various angler types (**Papers II & III**). For example, restrictive minimum-size limits are predicted lead to an under-representation of consumptive anglers relative to trophy anglers (**Paper II**). I also speculated in **Paper I** that the reduction in angler effort after the implementation of zero-harvest regulations was due to the loss of consumptive anglers from the system. However, without data on angler preferences this cannot be confirmed. Inequitable distributions in the composition of the anglers fishing has the potential to result in dissatisfaction with management actions by some angler types (Dorow et al. 2010), and produce conflict among angling groups.

Given the potentially inequitable distribution of resources in mixed-angler fisheries, the question thus arises what types of fishing opportunities should be provided and how should these be distributed (Driver et al. 1984, Cole and Ward 1994)? From an economics perspective what matters is the maximization of the social welfare a fishery provides, but this perspective overlooks that different angler types have competing interests. As long as alternative sites are available in a region, the displacement of one angler type by another might not matter if the effort redistribution is biologically sustainable. In this case, the repeated call to manage for diverse angling opportunities to enhance the recreational fishing experience of all anglers (Driver et al. 1984, Aas et al. 2000, Arlinghaus and Mehner 2004) may be the best strategy. My work is among the first to explicitly demonstrate the benefits of such an approach when determining optimal, angler-type-specific regulations that maximize social welfare. However, when fisheries resources are scarce in a region, managers might have difficulties jointly satisfying the interests of the entire angling public (Loomis and Ditton 1993, Daigle et al. 1996). In these situations, decisions may be needed about who and how many angler types may utilize scarce resources (Loomis and Ditton 1993, Daigle et al. 1996, Cox et al. 2003). Therefore, my results (**Papers II, III & IV**) highlight the need for managers to be clear about their management goals and objectives when implementing regulations (Barber and Taylor 1990, Aas and Ditton 1998, Fenichel et al. 2013b), particularly those that anglers perceive will or will constrain their angling activities.

4.2 The biological component

Historically, fisheries science has primarily focused on the dynamics of the production-side of the fishery system, the response of fish populations to exploitation, largely ignoring the dynamics of the consumers (Radomski et al. 2001, Cox and Walters 2002, Beard et al. 2003). Thus, it is well established that fish that exhibit different life-history strategies differ in their productivity and in their ability to compensate for changes in mortality due to fishing (Reynolds et al. 2001, Rose et al. 2001, Goodwin et al. 2006), and in the amount of fishing mortality species can sustain (Reynolds et al. 2001). However, past research has not examined the influence of fish life history on fish-angler interactions. Findings from **Papers III & IV** indicate that, for both the social and biological sustainability of recreational fisheries, the behaviour of anglers must be considered in the context of the LHTs they are fishing.

4.2.1 Biological sustainability

Papers III & IV indicate that LHTs differed in their intrinsic vulnerability to overexploitation, as expected Spawning-potential ratio, SPR, was used as the metric to assess the risk of recruitment overfishing. Larger-bodied LHTs (bull trout and pike) that were naturally less abundant were found to be more susceptible to overexploitation than the smaller-bodied, more productive LHTs (perch and brown trout). These results generally support empirical findings that species with "slow" life histories (i.e., those that mature late, with large maximum body sizes and low reproductive rates) are prone to greater population declines than species with the opposite characteristics (Jennings et al. 1998, Reynolds et al. 2001, Dulvy et al. 2003). Furthermore, my results give credence to the argument that, as a general "rule of thumb", maximum body size can provide an useful indicator of extinction vulnerability in the absence of more detailed biological information (Jennings et al. 1998, Reynolds et al. 2001, Dulvy et al. 2003), (but see Duncan and Lockwood 2001, Pinsky et al. 2011, Hutchings et al. 2012). However, my findings also caution that any classification based on specific life-history characteristics risks obscuring important differences in other life-history characteristics, resulting in erroneous predictions of species vulnerability. For example, I found that age-at-maturation, fecundity and natural mortality are unlikely to be good indicators of vulnerable LHTs, contrary to other studies (Jennings et al. 1998, Reynolds et al. 2001). Life-history strategies map onto a continuous and multi-dimensional plane (Rose et al. 2001), and there will likely always be exceptions to "the rule". Thus, whenever possible, quantitative modelling approaches should be used to predict the responses of fish populations to exploitation from angling.

Given that LHTs differ in their vulnerability, the question becomes how does this influence fish-angler interactions? **Paper II** established that who fishes, and how much angler types fish, has important consequences for the impact (in terms of SPR) that angling has on the fish population. This result is reinforced by results from **Papers III & IV**. For example, **Paper III** shows that the greatest impact on fish populations was by consumptive anglers under liberal minimum-size limits, while under more restrictive regulations it was by trophy anglers. However, a key finding of **Paper III** is that angler types likely respond differently to the various LHTs, with angler types being preferentially attracted to LHTs over others. This finding is supported by results from **Paper IV**, particularly by the substantial differences in optimal regulations of casual anglers among LHTs.

A further key finding of **Paper III** is that the relative importance of fishing practices and fishing preferences for determining angling impacts differ with LHT. For example, because of their propensity to voluntarily release fish, the impact of trophy anglers on intrinsically less vulnerable LHTs, such as brown trout, was much less than that of consumptive anglers under liberal regulations. Yet, when targeting intrinsically more vulnerable LHTs, all angler types had similar impacts under liberal regulations (**Paper III**). This is because catch rates were not sufficient to exceed even the low voluntary daily bag limit (1 fish every 2 days) set by trophy anglers. Instead, angler preferences became paramount in determining the impacts of angling on more vulnerable LHTs. Under more conservative regulations, angling effort by trophy anglers was predicted to be sufficient to result in the recruitment overfishing of the most vulnerable LHT, bull trout, at moderate license levels (**Paper III**), because of the tolerance of these anglers for restrictive regulations and the preferences for other fishery attributes that existed under these regulations. This unexpected outcome would not have come to light without an integrated modelling approach, such as the one used here. It illustrates the importance of using social-ecological models when making predictions about the impacts of management actions on the biological sustainability of recreational fisheries.

4.2.2 Social sustainability

LHT not only influences predictions about the impacts of angling on fish populations, but as **Papers III & IV** demonstrate, LHT can also have important consequences for how to manage fisheries in an optimal manner (from an OSY approach). In **Paper III**, I found that while optimal license numbers were generally unresponsive to the LHT being fished, optimal minimum-size limits increased dramatically with increased vulnerability of LHTs to overexploitation. However, in **Paper IV**, in which angler types were described based on results from a survey of real anglers, patterns were much less consistent. Similar to **Paper III**, optimal license numbers (when hooking mortality was absent) in **Paper IV** were generally similar across LHTs, except in the case of casual anglers. In the case of casual anglers optimal license numbers declined as the intrinsic vulnerability of the LHT increased; a pattern which also emerged for other angler types when cryptic mortality rates increased. Furthermore, in contrast to **Paper III**, the relationship between optimal MSL and LHT vulnerability in **Paper IV** was not consistent across angler types. These results in combination clearly demonstrate the need to consider both who is fishing and the target species when deriving socially optimal regulations. Yet, MSLs are often set based on simple criteria, ignoring the complexity of the attributes that contribute to angler utility. For

example, MSLs are often set as low as possible to minimize the loss of potential harvest to natural mortality (Johnson and Martinez 1995), but high enough to allow most fish to spawn at least once (Noble and Jones 1999). However, findings from **Papers III & IV** suggest that such low MSLs do not maximize social welfare, supporting concerns that such "one-size-fits-all" management policies can result in the socially suboptimal management of recreational fisheries and erode their ecological and social resilience (Carpenter and Brock 2004).

A key consideration for the social sustainability of recreational fisheries, evidenced by **Papers III & IV**, is that different angler types are implicitly attracted to different LHTs. Thus, my research suggests that fish LHT should play an important role when making decisions about which angler type(s) to manage a fishery for. For example, if the objective is to maximize social welfare, it makes little sense to manage a bull trout fishery for consumptive anglers, both from a biological and social perspective. Even under optimal regulation, consumptive anglers were likely to cause recruitment overfishing of bull trout, and gained much less welfare from targeting this species than the intrinsically less vulnerable LHTs which they inherently seemed to prefer (**Paper III**). While the management of certain species for certain angler types is not a new concept (Fisher 1997, Aas et al. 2000), the bioeconomic modelling approach, such as the one used in my research, allow managers to make transparent, defensible decisions in this regard (Fenichel et al. 2013b). The next step would be to develop a multispecies model, to account for the influence of species substitution on angler behaviour (Sutton and Ditton 2005, Gentner and Sutton 2008).

4.3 The management component

It has been suggested that optimum social yield (OSY) constitutes a superior approach to recreational fisheries management, compared to MSY, because it accounts for a broader range of biological, social and economic factors (Roedel 1975, Malvestuto and Hudgins 1996, Cox et al. 2003, Carpenter and Brock 2004). My research supports this paradigm shift. Optimal regulations resulted in the biological sustainability of the fishery (**Papers II, III & IV** when hooking mortality was $\leq$ 5%), in all but one case, a solely consumptive angler population targeting the particularly vulnerable LHT, bull trout. This occurred despite clear differences in the regulations that maximized angler utility among angler types and LHTs and despite the general decline in SPR levels under optimal regulations with LHT vulnerability. My work suggests that socioeconomic management objectives, such as maximizing social welfare, can account for the state of a fish population through its influence on angler utility

(i.e., correlations between fish population abundance and catch-related attributes of the fishery). In line with the precautionary approach to fisheries management (FAO 2012), predictions of optimal regulations that result in conditions that approach recruitment overfishing should be treated with caution to account for margins of error and stochastic processes that underlie any fishery. However, generally, the management advice provided when using an OSY approach to recreational fisheries management resulted in both socially and biologically sustainable exploitation. Furthermore, management for OSY provides a clear objective against which the success of management actions can be judged (Fenichel et al. 2013b).

What remains unclear is how alterations of the management component, namely – the type of regulations used, the effectiveness of angling regulations, and the influence of alternative management objectives on the derivation of optimal regulations – influence the results previously discussed. Thus, I dedicate this section to that discussion.

4.3.1 Biological sustainability

The effectiveness of management regulations, in terms of maintaining a biologically sustainable population and meeting other conservation objectives, depends on their ability to limit mortality caused by fishing. This can be done either by limiting the number of anglers fishing (input regulations) and, thus, the number of fish caught, or by limiting the number of fish harvested (output regulations). However, some harvest regulations may be more effective at mitigating the negative impacts of fishing than others. **Paper V** indicates that, compared to MSLs, harvest-slot limits (HSs), that protect both large and small individuals but allow the harvest of intermediate size classes, were generally more successful at conserving reproductive biomass (i.e., high SPR) and minimizing the truncation of the natural age and size structure of the stock that fishing inevitably causes (Hutchings and Reynolds 2004, Lewin et al. 2006). This is an important result because the removal of old, large, and hence more fecund fish can erode the compensatory capacity of the population (Birkeland and Dayton 2005, Lorenzen 2008, Arlinghaus et al. 2010). Such juvenescence of exploited populations can increase population variability and reduce their ability to offset environmental variation through bet-hedging strategies (Berkeley et al. 2004, Anderson et al. 2008, Hsieh et al. 2010). Furthermore, changes in larval quality and offspring survival (e.g., because of spawning timing) with age or size of the female can limit recruitment (Scott et al. 1999, Berkeley et al. 2004, Birkeland and Dayton 2005, O'Farrell and Botsford 2006). These

processes were not explicitly modeled in **Paper V**, yet concerns about changes in the age and stage structure of the fish populations have led to a general push towards a more precautionary form of fisheries management which maintains old-growth age structure in fish populations (Francis et al. 2007, Hsieh et al. 2010, Zhou et al. 2010), including more specifically the management of freshwater recreational species such as pike (Arlinghaus et al. 2010) and walleye (Venturelli et al. 2010).

All harvest regulations, however, implicitly assume that a substantial proportion of released fish survive and that anglers are compliant with the regulations. My research (**Papers IV & V**) shows that, depending on the LHT being exploited and the composition of the angler population, hooking mortality and regulatory noncompliance can severely undermine the efficacy of angling regulations in terms of biological conservation, in some cases even when the fishery is managed in a socially optimal manner. **Paper IV** and other studies (e.g., Post et al. 2003, Coggins et al. 2007, Pine et al. 2008) demonstrate the even low levels of hooking mortality that are commonly reported in the literature (e.g., 57.1% of estimates ≤ 10%, Hühn and Arlinghaus 2011) are sufficient to cause recruitment overfishing of intrinsically more vulnerable LHTs. More resilient LHTs, however, only experience such negative effects when hooking mortality levels were extremely high (50% in **Paper IV**), levels which are rarely reported in the literature (e.g., 7.9 % of estimates ≥ 50%, Hühn and Arlinghaus 2011). Furthermore, my work is the first to demonstrate that the composition of the angler population is also important in this context. For example, only the most committed anglers caused recruitment overfishing of the most resilient LHT, even when hooking mortality was 50% (**Paper IV**).

In terms of the efficacy of regulations, an additional novel finding of **Paper IV**, was the importance of modeling regulatory noncompliance as a depensatory process (Allee effect). In contrast to other studies that modelled noncompliance as a constant rate (e.g., Gigliotti and Taylor 1990, Post et al. 2003), I found that noncompliance generally only affected the biological outcome, in terms of recruitment overfishing, of the most intrinsically vulnerable LHTs, and only when levels of hooking mortality were low (< 25%). It was only under these circumstances that catch rates were sufficiently low to produce a strong depensatory effect in noncompliance (i.e., levels of noncompliance > 5%). It was also only under these circumstances that other sources of mortality – harvest and hooking mortality – were sufficiently low that the population was not already recruitment overfished even when noncompliance mortality was absent. While these results may suggest that noncompliance

can be disregarded, the intermediate range of MSLs at which consideration of noncompliance can be critical is generally the range of MSLs utilized in recreational fisheries. This is particularly important if input regulations are not feasible such as would occur in open-access fisheries. Furthermore, **Paper IV** indicates that ignoring the presence of cryptic mortality when deriving optimal regulations results in recruitment overfishing of all but the most resilient LHTs by most angler types, and in the case of the intrinsically vulnerable LHTs, even when hooking mortality rates were at levels commonly reported in the literature (e.g., means of 18% and 15.9% across studies, Bartholomew and Bohnsack 2005, Hühn and Arlinghaus 2011, respectively). This has important implications, particularly for species-at-risk, suggesting that efforts should be directed towards gaining accurate estimates of cryptic mortality for species whose life-history characteristics make them particularly vulnerable to overfishing.

4.3.2 Social sustainability

Cryptic mortality also had important implications for the social sustainability of recreational fisheries. In **Paper IV**, I found that cryptic mortality broadly contributes to the erosion of the social welfare derived from most recreational fisheries, something that to my knowledge has not been evaluated in other studies. It should be pointed out however, that LHT and composition of the angler population were important for determining the degree to which angler welfare was reduced. Such welfare loss suggests that the welfare benefits associated with minimizing cryptic mortality can be large, and thus such actions are in the self-interest of anglers. Hence, if maximizing angler satisfaction is a priority of recreational managers, a focus should be placed on minimizing hooking mortality through such methods as gear restrictions, and education and outreach programs designed to reduce handling stress and injury because these actions increase post-release survival in most fish species (Arlinghaus et al. 2007, EIFAC 2008, FAO 2012).

The efficacy of angling regulations for achieving social sustainability will also be influenced by management objectives. Management objectives will influence which normative criteria (e.g., individual utilities) are considered and how they are weighted and aggregated in the social welfare function (also referred to as score function) used to quantify OSY (Fenichel et al. 2013b). It is assumed that any concerns about equity are accounted for in the aggregation method (Perman et al. 2003). However, maximizing social welfare does not necessarily result in an equitable distribution of resources among individuals (Perman et al. 2003, Fenichel et

al. 2013b), as I found in **Papers II & III**. Furthermore, there is no universal consensus on which normative criteria to use and how to weight and aggregate them (Perman et al. 2003, Fenichel et al. 2013b). Thus, the outcomes of three alternative management objectives were investigated in both **Paper II** and **Paper V**. **Paper II** demonstrates that different management objectives for mixed angler populations, ranging from a utilitarian objective that maximizes angler participation and overall satisfaction (both of which are potential objectives for recreational fisheries, Bennett et al. 1978), to a more equitable utilitarian objective that weights angler utility equally (because a more equitable distribution of resources may be desired, Loomis and Ditton 1993), to a Rawlsian objective that maximizes the participation and satisfaction of the least-satisfied group (Perman et al. 2003), result in different predictions about optimal regulations. The more equitable management objectives resulted in more restrictive optimal regulations but also attracted a more diverse composition of anglers to the fishery (**Paper II**).

Paper V used a different approach. Rather than explicitly weighting the interests of different angler types, it weighed the value of harvest and trophy catch differently to produce three score functions – one that emphasized harvest, one that emphasized trophy catch, and a compromise function that weighted harvest and trophy catch equally. **Paper V** demonstrated, for both HSLs (harvest-slot limits) and MSLs, that more liberal regulations achieved harvest-dominated objectives, more conservative regulations achieved trophy catch-dominated objectives, and the regulations achieving compromise objectives were intermediate. Perhaps a more interesting result from **Paper V** is that regardless of the management objective, optimal HSLs provided both greater harvest and trophy catch when compared to optimal MSLs. Furthermore, optimal HSLs generally resulted in less recruitment overfishing, caused less size truncation, and were less deleteriously affected by hooking mortality. It should be noted however these benefits came at the cost of fishery yield and the size of fish harvested. If harvest and trophy catch are important contributors of angler utility, results from **Paper V** imply that HSLs may in fact provide greater social welfare to the angling community than MSLs, although this would have to be formally examined. This is an interesting finding, given that slot limits which are much less commonly implemented than MSLs (Radomski et al. 2001). Perhaps due to the complexity/unfamiliarity of slot limits, noncompliance with them is often greater than would be expected with MSLs (Pierce and Tomcko 1998, Sullivan 2002, Caroffino 2013), a factor that could undermine the previously stated benefits of HSLs for social welfare. In combination, results from **Papers II & V** illustrate that managers need

to ensure that the score function (welfare function) applied closely reflects their management objectives, when implementing an OSY approach to recreational-fisheries management, and that the appropriate type of regulation is implemented to achieve these objectives.

5 CONCLUSIONS

The objective of my doctoral research was to evaluate the importance of jointly considering the social, biological, and management components of recreational fisheries for the biologically and socially sustainable management of recreational fisheries. While such interdisciplinary research has been rare historically, interest in modeling angler behaviour to inform recreational fisheries management has increased since I began my doctoral work, and my research has been cited as making a key contribution to this area of research (Fenichel et al. 2013a). The research presented here is by no means an exhaustive examination of all factors affecting recreational fisheries, or even all factors that fall within the components I examined. However, the goal of this research was to gain insights into the importance of considering and the potential problems with omitting or underrepresenting these components for the sustainable management of recreational fisheries, and to spur on future research.

The questions of who to manage a fishery for and which management objective is appropriate are open for debate, and will likely vary from fishery to fishery based on individual differences in the social-ecological system. However, the results of my doctoral research demonstrate that interdisciplinary bioeconomic models, such as mine, can be used by managers to predict the effects of management actions on different segments of the angler community, and to quantify any welfare changes that result. Furthermore, with a basis of clear objectives and quantitative descriptions of angler behaviour, managers can make transparent and defensible resource allocation decisions which consider the potential consequences of management actions on both the fish and angling populations. To this end, current monitoring methods need to be modified so that they may better identify and describe angler diversity, allowing managers to better understand who is fishing and why. Accounting for angler dynamics and angler diversity in fisheries-management models, and appropriately tailoring models to the LHT of the target species, will provide more accurate predictions about which regulations minimize the biological impacts of angling, maximize angler satisfaction, and ideally will identify and minimize conflicts among angling groups. With such an integrated understanding I am hopeful that we can progress towards socially and biologically sustainable management of recreational fisheries.

ACKNOWLEDGEMENTS

Financial support for my research was provided by the Gottfried-Wilhelm-Leibniz Community through the Adaptfish Project (www.adaptfish.igb-berlin.de). Additional funding was received from the German Ministry for Education and Research (BMBF) through the Program for Social-Ecological Research Besatzfisch-Project (www.besatz-fisch.de). Furthermore, I would like to acknowledge support from the Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin, Germany, and the International Institute for Applied Systems Analysis (IIASA), Laxenburg, Austria.

I would also like to take this opportunity to thank people that assisted me on this journey. First and foremost, I would like to thank my supervisor and mentor, Prof. Dr. Robert Arlinghaus, who gave me the opportunity to embark on this adventure, and provided me with numerous opportunities I never would have experienced otherwise. Being exposed to such a multi-disciplinary research group, such as Adaptfish and later Besatzfisch (www.besatz-fisch.de), has broadened my scientific perspective. His love for the field of recreational fisheries and amazing breadth of knowledge continue to be an inspiration. I have always enjoyed my discussions with him, and thank him for all of his valuable insights, advice, and particularly for all of his patience in seeing this thesis to its fruition. He has always been very understanding, and I recognize and appreciate that.

I would also like to thank my supervisor from the IIASA, Dr. Ulf Dieckmann. Thank you for introducing me to the world of fisheries modelling, and for your guidance in figuring out at least some of its mysteries. The opportunity to work at IIASA and to be involved, at least peripherally, with the Marie Curie Research Training Network on Fisheries Induced Adaptive Changes in Exploited Stocks (FishACE) and the Specific Targeted Research Project on Fisheries Induced Evolution (FinE) under the European Community's Sixth Framework Program were invaluable.

To my colleagues, both at IGB and IIASA, I thank you for all your support. In particular, I would like to thank Shuichi Matsumura (IIASA, IGB), Thomas Klefoth (IGB), Ben Beardmore (SFU), Katja Enberg (IIASA), Rupert Mazzucco (IIASA), and Jacob Johansson (IIASA) for all their discussions and insights about my research. I would also like to give special thanks to my dear friends Silva Uusi-Heikkilä and Katrin Daedlow at IGB, and to Davnah Payne, Barbara Fischer, and Rebecca Whitlock at IIASA. I could not have done this

without the support of these truly amazing ladies, and scientists. Thanks for being there through it all.

Finally, I would like to thank my family. To my twin boys, Felix and Xavi, thank you for inspiring me every day to see the world just a little differently and to keep things in perspective. To my parents and sister, I never could have done this without your steady support over the years, and teaching me that I can achieve things that I set my mind to. Last but not least, I would like to thank my husband, Ché, whose constant encouragement and the sacrifices that he made on my behalf are responsible for me being where I am today.

REFERENCES

Aas, Ø., and R. B. Ditton. 1998. Human dimensions perspective on recreational fisheries management: implications for Europe.*in* P. Hickley and H. Tompkins, editors. Recreational Fisheries: Social, Economic and Management Aspects. Blackwell Scientific Publications, Oxford, U.K.

Aas, Ø., W. Haider, and L. Hunt. 2000. Angler responses to potential harvest regulations in a Norwegian sport fishery: a conjoint-based choice modeling approach. North American Journal of Fisheries Management **20**:940-950.

Allen, M. S., R. N. M. Ahrens, M. J. Hansen, and R. Arlinghaus. 2013. Dynamic angling effort influences the value of minimum-length limits to prevent recruitment overfishing. Fisheries Management and Ecology **20**:247-257.

Allen, M. S., P. Brown, J. Douglas, W. Fulton, and M. Catalano. 2009. An assessment of recreational fishery harvest policies for Murray cod in southeast Australia. Fisheries Research **95**:260-267.

Allen, M. S., C. J. Walters, and R. Myers. 2008. Temporal trends in largemouth bass mortality, with fishery implications. North American Journal of Fisheries Management **28**:418-427.

Allendorf, F. W., and J. J. Hard. 2009. Human-induced evolution caused by unnatural selection through harvest of wild animals. Proceedings of the National Academy of Sciences **106**:9987-9994.

Almodóvar, A., and G. G. Nicola. 2004. Angling impact on conservation of Spanish stream-dwelling brown trout *Salmo trutta*. Fisheries Management and Ecology **11**:173-182.

Anderson, C. N. K., C. H. Hsieh, S. A. Sandin, R. Hewitt, A. Hollowed, J. Beddington, R. M. May, and G. Sugihara. 2008. Why fishing magnifies fluctuations in fish abundance. Nature **452**:835-839.

Anderson, L. G. 1993. Toward a complete economic theory of the utlization and management of recreational fisheries. Journal of Environmental Economics and Management **24**:272-295.

Arlinghaus, R. 2007. Voluntary catch-and-release can generate conflict within the recreational angling community: a qualitative case study of specialised carp, *Cyprinus carpio*, angling in Germany. Fisheries Management and Ecology **14**:161-171.

Arlinghaus, R., M. Bork, and E. Fladung. 2008. Understanding the heterogeneity of recreational anglers across an urban-rural gradient in a metropolitan area (Berlin, Germany), with implications for fisheries management. Fisheries Research **92**:53-62.

Arlinghaus, R., and S. J. Cooke. 2009. Recreational fisheries: socioeconomic importance, conservation issues and management challenges. Pages 39-58 *in* B. Dickson, J. Hutton, and B. Adams, editors. Recreational hunting, conservation and rural livelihoods: science and practice. Blackwell Publishing, Oxford, U.K.

Arlinghaus, R., S. J. Cooke, J. Lyman, D. Policansky, A. Schwab, C. Suski, S. G. Sutton, and E. B. Thorstad. 2007. Understanding the complexity of catch-and-release in recreational fishing: an integrative synthesis of global knowledge from historical, ethical, social and biological perspectives. Reviews in Fisheries Science **15**:75-167.

Arlinghaus, R., S. Matsumura, and U. Dieckmann. 2010. The conservation and fishery benefits of protecting large pike (*Esox lucius* L.) by harvest regulations in recreational fishing. Biological Conservation **143**:1444-1459.

Arlinghaus, R., and T. Mehner. 2004. A management-orientated comparative analysis of urban and rural anglers living in a metropolis (Berlin, Germany). Environmental Management **33**:331-344.

Arlinghaus, R., T. Mehner, and I. G. Cowx. 2002. Reconciling traditional inland fisheries management and sustainability in industrialized countries, with emphasis on Europe. Fish and Fisheries **3**:261-316.

Baccante, D. 1995. Assessing catch inequality in walleye angling fisheries. North American Journal of Fisheries Management **15**:661-665.

Barber, W. E., and J. N. Taylor. 1990. The importance of goals, objectives, and values in the fisheries management process and organization: a review. North American Journal of Fisheries Management **10**:365-373.

Bartholomew, A., and J. Bohnsack. 2005. A review of catch-and-release angling mortality with implications for no-take reserves. Reviews in Fish Biology and Fisheries **15**:129-154.

Beard, T. D., Jr., S. P. Cox, and S. R. Carpenter. 2003. Impacts of daily bag limit reductions on angler effort in Wisconsin walleye lakes. North American Journal of Fisheries Management **23**:1283-1293.

Beardmore, B., W. Haider, L. M. Hunt, and R. Arlinghaus. 2011. The importance of trip context for determining primary angler motivations: are more specialized anglers more catch-oriented than previously believed? North American Journal of Fisheries Management **31**:861-879.

Beardmore, B., W. Haider, L. M. Hunt, and R. Arlinghaus. 2013. Evaluating the ability of specialization indicators to explain fishing preferences. Leisure Sciences **35**:273-292.

Bennett, D. H., E. L. Hampton, and R. T. Lackey. 1978. Current and future fisheries management goals: implications for future management. Fisheries **3**:10-14.

Berkeley, S. A., M. A. Hixon, R. J. Larson, and M. S. Love. 2004. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. Fisheries **29**:23-32.

Birkeland, C., and P. K. Dayton. 2005. The importance in fishery management of leaving the big ones. Trends in Ecology and Evolution **20**:356-358.

Bryan, H. 1977. Leisure value systems and recreational specialization: the case of trout fishermen. Journal of Leisure Research **9**:174-187.

Carlin, C., S. A. Schroeder, and D. C. Fulton. 2012. Site choice among Minnesota walleye anglers: the influence of resource conditions, regulations and catch orientation on lake preference. North American Journal of Fisheries Management **32**:299-312.

Caroffino, D. C. 2013. Angler compliance with lake trout length limit regulations in Great Lakes waters. North American Journal of Fisheries Management **33**:1203-1209.

Carpenter, S. R., and W. A. Brock. 2004. Spatial complexity, resilience, and policy diversity: fishing on lake-rich landscapes. Ecology and Society **9**:8 [online]. Available from www.ecologyandsociety.org/vol9/iss1/art8/.

Coggins, L. G., Jr., M. J. Catalano, M. S. Allen, W. E. Pine, III, and C. J. Walters. 2007. Effects of cryptic mortality and the hidden costs of using length limits in fishery management. Fish and Fisheries **8**:196-210.

Cole, R. A., and F. A. Ward. 1994. Optimum Fisheries Management Policy: Angler Opportunity versus Angler Benefit. North American Journal of Fisheries Management **14**:22-33.

Coleman, F. C., W. F. Figueira, J. S. Ueland, and L. B. Crowder. 2004. The impact of United States recreational fisheries on marine fish populations. Science **305**:1958-1960.

Cook, M. F., T. J. Goeman, P. J. Radomski, J. A. Younk, and P. C. Jacobson. 2001. Creel limits in Minnesota: a proposal for change. Fisheries **26**:19-26.

Cooke, S. J., and I. G. Cowx. 2004. The role of recreational fisheries in global fish crises. Bioscience **54**:857-859.

Cooke, S. J., and I. G. Cowx. 2006. Contrasting recreational and commercial fishing: Searching for common issues to promote unified conservation of fisheries resources and aquatic environments. Biological Conservation **128**:93-108.

Cox, S., and C. Walters. 2002. Maintaining quality in recreational fisheries: how success breeds failure in management of open-access sport fisheries. Pages 107-119 *in* T. J. Pitcher and C. E. Hollingworth, editors. Recreational Fisheries: Ecological, Economic and Social Evaluation. Blackwell Publishing, Oxford, U.K.

Cox, S. P., T. D. Beard, and C. Walters. 2002. Harvest control in open-access sport fisheries: hot rod or asleep at the reel? Bulletin of Marine Science **70**:749-761.

Cox, S. P., C. J. Walters, and J. R. Post. 2003. A model-based evaluation of active management of recreational fishing effort. North American Journal of Fisheries Management **23**:1294-1302.

Daigle, C. P., D. K. Loomis, and R. B. Ditton. 1996. Procedural justice in fishery resource allocations. Fisheries **21**:18-23.

Die, D. J., V. R. Restrepo, and J. M. Hoenig. 1988. Utility-per-recruit modelling: A neglected concept. Transactions of the American Fisheries Society **117**:274-281.

Ditton, R. B., D. K. Loomis, and S. Choi. 1992. Recreational specialization: re-conceptualization from a social worlds perspective. Journal of Leisure Research **24**:35-51.

Dorow, M., B. Beardmore, W. Haider, and R. Arlinghaus. 2010. Winners and losers of conservation policies for European eel, *Anguilla anguilla*: an economic welfare analysis for differently specialised eel anglers. Fisheries Management and Ecology **17**:106-125.

Dorr, B., I. A. Munn, and K. O. Meals. 2002. A socioeconomic and biological evaluation of current and hypothetical crappie regulations in Sardis Lake, Mississippi: an integrated approach. North American Journal of Fisheries Management **22**:1376-1384.

Driver, B. L., C. Phillips, E. P. Bergersen, and C. C. Harris. 1984. Using angler preference data in defining types of sport fisheries to manage. Transactions of the North American Wildlife and Natural Resources Conference (USA) **49**:82-90.

Dulvy, N. K., Y. Sadovy, and J. D. Reynolds. 2003. Extinction vulnerability in marine populations. Fish and Fisheries **4**:25-64.

Duncan, J. R., and J. L. Lockwood. 2001. Extinction in a field of bullets: a search for causes in the decline of the world's freshwater fishes. Biological Conservation **102**:97-105.

EIFAC. 2008. (European Inland Fisheries Advisory Commission, FAO). EIFAC Code of Practice for Recreational Fisheries. EIFAC Occasional Paper. No. 42. FAO, Rome. 45 pp.

FAO. 2012. (Food and Agricultural Organization of the United Nations). FAO Technical Guidelines for Responsible Fisheries: Recreational Fisheries. No. 13. FAO, Rome. 176 pp.

Fayram, A. H., M. J. Hansen, and T. J. Ehlinger. 2006. Influence of walleye stocking on angler effort in Wisconsin. Human Dimensions of Wildlife **11**:129-141.

Fayram, A. H., and P. J. Schmalz. 2006. Evaluation of a modified bag limit for walleyes in Wisconsin: effects of decreased angler effort and lake selection. North American Journal of Fisheries Management **26**:606-611.

Fenichel, E. P., J. K. Abbott, and B. Huang. 2013a. Modelling angler behaviour as a part of the management system: synthesizing a multi-disciplinary literature. Fish and Fisheries **14**:137-157.

Fenichel, E. P., B. Gentner, and R. Arlinghaus. 2013b. Normative considerations for recreational fishery management: a bioeconomic framework for linking positive science and normative fisheries policy decisions. Fisheries Management and Ecology **20**:223-233.

Ferter, K., T. Borch, J. Kolding, and J. H. Vølstad. 2013. Angler behaviour and implications for management - catch-and-release among marine angling tourists in Norway. Fisheries Management and Ecology **20**:137-147.

Fisher, M. R. 1997. Segmentation of the angler population by catch preference, participation, and experience: a management-oriented application of recreation specialization. North American Journal of Fisheries Management **17**:1-10.

Francis, R. C., M. A. Hixon, M. E. Clarke, S. A. Murawski, and S. Ralston. 2007. Ten commandments for ecosystem-based fisheries scientists. Fisheries **32**:217-233.

Fulton, E. A., A. D. M. Smith, D. C. Smith, and I. E. van Putten. 2011. Human behaviour: the key source of uncertainty in fisheries management. Fish and Fisheries **12**:2-17.

Gentner, B., and S. Sutton. 2008. Substitution in recreational fishing. Pages 150-169 *in* Ø. Aas, editor. Global Challenges in Recreational Fisheries. Blackwell Publishing Ltd.

Gigliotti, L. M., and W. W. Taylor. 1990. The effect of illegal harvest on recreational fisheries. North American Journal of Fisheries Management **10**:106-110.

Goodwin, N. B., A. Grant, A. L. Perry, N. K. Dulvy, and J. D. Reynolds. 2006. Life history correlates of density-dependent recruitment in marine fishes. Canadian Journal of Fisheries and Aquatic Sciences **63**:494-509.

Hahn, J. 1991. Angler specialization: measurement of a key sociological concept and implications for fisheries management decisions. American Fisheries Society Symposium **12**:380-389.

Heermann, L., M. Emmrich, M. Heynen, M. Dorow, U. König, J. Borcherding, and R. Arlinghaus. 2013. Explaining recreational angling catch rates of Eurasian perch, Perca fluviatilis: the role of natural and fishing-related environmental factors. Fisheries Management and Ecology **20**:187-200.

Heino, M., and O. R. Godø. 2002. Fisheries-induced selection pressures in the context of sustainable fisheries. Bulletin of Marine Science **70**:639-656.

Hilborn, R. 2007. Defining success in fisheries and conflicts in objectives. Marine Policy **31**:153-158.

Hilborn, R., and C. Walters. 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty. Chapman Hall, New York.

Homans, F. R., and J. A. Ruliffson. 1999. The effects of minimum size limits on recreational fishing. Marine Resource Economics **14**:1-14.

Hsieh, C. H., A. Yamauchi, T. Nakazawa, and W. F. Wang. 2010. Fishing effects on age and spatial structures undermine population stability of fishes. Aquatic Sciences **72**:165-178.

Hühn, D., and R. Arlinghaus. 2011. Determinants of hooking mortality in freshwater recreational fisheries: a quantitative meta-analysis. American Fisheries Society Symposium **75**:141-170.

Hunt, L. 2005. Recreational fishing site choice models: insights and future opportunities. Human Dimensions of Wildlife **10**:153-172.

Hunt, L. M., R. Arlinghaus, N. Lester, and R. Kushneriuk. 2011. The effects of regional angling effort, angler behavior, and harvesting efficiency on landscape patterns of overfishing. Ecological Applications **21**:2555-2575.

Hutchings, J. A., R. A. Myers, V. B. García, L. O. Lucifora, and A. Kuparinen. 2012. Life-history correlates of extinction risk and recovery potential. Ecological Applications **22**:1061-1067.

Hutchings, J. A., and J. D. Reynolds. 2004. Marine fish population collapses: consequences for recovery and extinction risk. Bioscience **54**:297-309.

Irwin, B. J., M. J. Wilberg, M. L. Jones, and J. R. Bence. 2011. Applying structured decision making to recreational fisheries management. Fisheries **36**:113-122.

Jacobson, P. C. 1996. Trophy and consumptive value-per-recruit analysis for a walleye fishery. North American Journal of Fisheries Management **16**:75-80.

Jennings, S., J. D. Reynolds, and S. C. Mills. 1998. Life history correlates of responses to fisheries exploitation. Proceedings of the Royal Society of London. Series B: Biological Sciences **265**:333-339.

Johnson, B. M., and S. R. Carpenter. 1994. Functional and numerical responses: a framework for fish-angler interactions? Ecological Applications **4**:808-821.

Johnson, B. M., and P. J. Martinez. 1995. Selecting harvest regulations for recreational fisheries: opportunities for research/management cooperation. Fisheries **20**:22-29.

Lester, N. P., T. R. Marshall, K. Armstrong, W. I. Dunlop, and B. Ritchie. 2003. A broad scale approach to management of Ontario's recreational fisheries. North American Journal of Fisheries Management **23**:1312-1328.

Lewin, W. C., R. Arlinghaus, and T. Mehner. 2006. Documented and potential biological impacts of recreational fishing: insights for management and conservation. Reviews in Fisheries Science **14**:305-367.

Loomis, D. K., and R. B. Ditton. 1993. Distributive justice in fisheries management. Fisheries **18**:14-18.

Lorenzen, K. 2008. Fish population regulation beyond stock and recruitment: the role of density-dependent growth in the recruited stock. Bulletin of Marine Science **83**:181-196.

Lorenzen, K., and K. Enberg. 2002. Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. Proceedings of the Royal Society of London, Series B **269**:49-54.

Malvestuto, S. P., and M. D. Hudgins. 1996. Optimum yield for recreational fisheries management. Fisheries **21**:6-17.

Manski, C. F. 1977. The structure of random utility models. Theory and Decision **8**:229-254.

Massey, D. M., S. C. Newbold, and B. Gentner. 2006. Valuing water quality changes using a bioeconomic model of a coastal recreational fishery. Journal of Environmental Economics and Management **52**:482-500.

McConnell, K. E., and J. G. Sutinen. 1979. Bioeconomic models of marine recreational fishing. Journal of Environmental Economics and Management **6**:127-139.

McFadden, D. 1974. Conditional logit analysis of quantitative choice behavior. Pages 105-142 *in* P. Zarembka, editor. Frontiers in econometrics. Academic Press Inc., New York, NY, USA.

McPhee, D. P., D. Leadbitter, and G. A. Skilleter. 2002. Swallowing the bait: is recreational fishing in Australia ecologically sustainable? Pacific Conservation Biology **8**:40-51.

Metcalf, S. J., K. Moyle, and D. J. Gaughan. 2010. Qualitative analysis of recreational fisher response and the ecosystem impacts of management strategies in a data-limited situation. Fisheries Research **106**:289-297.

Näslund, I., T. Eriksson, D. Hannersjö, L. Bergwall, G. Jacobsson, and K. Leonardsson. 2010. Time trends in angler compliance with harvest regulations in stream fisheries. Fisheries Management and Ecology **17**:52-62.

Noble, R. L., and T. W. Jones. 1999. Managing fisheries with regulations. Pages 455-477 *in* C. C. Kohler and W. A. Hubert, editors. Inland fisheries management in North America, 2nd edition. American Fisheries Society, Bethesda, MD.

O'Farrell, M. R., and L. W. Botsford. 2006. The fisheries management implications of maternal-age-dependent larval survival. Canadian Journal of Fisheries and Aquatic Sciences **63**:2249-2258.

Oh, C.-O., R. B. Ditton, D. K. Anderson, D. Scott, and J. R. Stoll. 2005a. Understanding differences in nonmarket valuation by angler specialization level. Leisure Sciences **27**:263-277.

Oh, C.-O., R. B. Ditton, B. Gentner, and R. Riechers. 2005b. A stated preference choice approach to understanding angler preferences for management options. Human Dimensions of Wildlife **10**:173-186.

Oh, C. O., and R. B. Ditton. 2006. Using recreation specialization to understand multi-attribute management preferences. Leisure Sciences **28**:369-384.

Page, K. S., G. C. Grant, P. Radomski, T. S. Jones, and R. E. Bruesewitz. 2004. Fish total length measurement error for recreational anglers: Causes and contribution to noncompliance fo the Mille Lacs walleye fishery. North American Journal of Fisheries Management **24**:939-951.

Page, K. S., and P. Radomski. 2006. Compliance with sport fishery regulations in Minnesota as related to regulation awareness. Fisheries **31**:166-178.

Parkinson, E. A., J. R. Post, and S. P. Cox. 2004. Linking the dynamics of harvest effort to recruitment dynamics in a multistock, spatially structured fishery. Canadian Journal of Fisheries and Aquatic Sciences **61**:1658-1670.

Paukert, C. P., J. A. Klammer, R. B. Pierce, and T. D. Simonson. 2001. An overview of northern pike regulations in North America. Fisheries **26**:6-13.

Paul, A. J., J. R. Post, and J. D. Stelfox. 2003. Can anglers influence the abundance of native and nonnative salmonids in a stream from the Canadian Rocky Mountains? North American Journal of Fisheries Management **23**:109-119.

Perman, R., Y. Ma, J. McGilvray, and M. Common. 2003. Natural resource and environmental economics. Third edition. Pearson Education Limited, Harlow, Essex, UK.

Peterson, J. T., and J. W. Evans. 2003. Quantitative decision analysis for sport fisheries management. Fisheries **28**:10-21.

Pierce, R. B. 2010. Long-term evaluations of length limit regulations for northern pike in Minnesota. North American Journal of Fisheries Management **30**:412-432.

Pierce, R. B., and C. M. Tomcko. 1998. Angler noncompliance with slot length limits for northern pike in five small Minnesota lakes. North American Journal of Fisheries Management **18**:720-724.

Pigliucci, M. 2005. Evolution of phenotypic plasticity: where are we going now? Trends in Ecology and Evolution **20**:481-486.

Pine, W. E., III, S. J. D. Martell, O. P. Jensen, C. J. Walters, and J. F. Kitchell. 2008. Catch-and-release and size limit regulations for blue, white, and striped marlin: the role of postrelease survival in effective policy design. Canadian Journal of Fisheries and Aquatic Sciences **2008**:5.

Pinsky, M. L., O. P. Jensen, D. Ricard, and S. R. Palumbi. 2011. Unexpected patterns of fisheries collapse in the world's oceans. Proceedings of the National Academy of Sciences **108**:8317-8322.

Post, J. R. 2013. Resilient recreational fisheries or prone to collapse? A decade of research on the science and management of recreational fisheries. Fisheries Management and Ecology **20**:99-110.

Post, J. R., C. Mushens, A. Paul, and M. Sullivan. 2003. Assessment of alternative harvest regulations for sustaining recreational fisheries: model development and application to bull trout. North American Journal of Fisheries Management **23**:22-34.

Post, J. R., and E. A. Parkinson. 2012. Temporal and spatial patterns of angler effort across lake districts and policy options to sustain recreational fisheries. Canadian Journal of Fisheries and Aquatic Sciences **69**:321-329.

Post, J. R., L. Persson, E. A. Parkinson, and T. van Kooten. 2008. Angler numerical response across landscapes and the collapse of freshwater fisheries. Ecological Applications **18**:1038-1049.

Post, J. R., M. Sullivan, S. Cox, N. P. Lester, C. J. Walters, E. A. Parkinson, A. J. Paul, L. Jackson, and B. J. Shuter. 2002. Canada's recreational fisheries: the invisible collapse? Fisheries **27**:6-17.

Radomski, P. 2003. Initial attempts to actively manage recreational fishery harvest in Minnesota. North American Journal of Fisheries Management **23**:1329-1342.

Radomski, P. J., and T. J. Goeman. 1996. Decision making and modeling in freshwater sport-fisheries management. Fisheries **21**:14-21.

Radomski, P. J., G. C. Grant, P. C. Jacobson, and M. F. Cook. 2001. Visions for recreational fishing regulations. Fisheries **26**:7-18.

Reynolds, J. D. 2003. Life histories and extinction risk. Pages 195-217 *in* T. M. Blackburn and K. J. Gaston, editors. Macroecology. Blackwell Publishing, Oxford, UK.

Reynolds, J. D., S. Jennings, and N. K. Dulvy. 2001. Life histories of fishes and population response to exploitation. Pages 147-168 *in* J. D. Reynolds, G. M. Mace, K. H. Redford, and J. G. Robinson, editors. Conservation of Exploited Species. Cambridge University Press, Cambridge, UK.

Reynolds, J. D., T. J. Webb, and L. A. Hawkins. 2005. Life history and ecological correlates of extinction risk in European freshwater fishes. Canadian Journal of Fisheries and Aquatic Sciences **692**:854-862.

Roedel, P. M. 1975. A summary and critique of the symposium on optimal sustainable yield. Pages 79-89 Optimum Sustainable Yield as a Concept in Fisheries Management. American Fisheries Society, Bethesda, MD.

Rose, K. A., J. H. Cowan, Jr., K. O. Winemiller, R. A. Myers, and R. Hilborn. 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. Fish and Fisheries **2**:293-327.

Scott, B., G. Marteinsdóttir, and P. Wright. 1999. Potential effects of maternal factors on spawning stock-recruitment relationships under varying fishing pressure. Canadian Journal of Fisheries and Aquatic Sciences **56**:1882-1890.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, UK.

Sullivan, M. G. 2002. Illegal angling harvest of walleyes protected by length limits in Alberta. North American Journal of Fisheries Management **22**:1053-1063.

Sutton, S. G., and R. B. Ditton. 2005. The substitutability of one type of fishing for another. North American Journal of Fisheries Management **25**:536-546.

van Poorten, B. T., S. P. Cox, and A. B. Cooper. 2013. Efficacy of harvest and minimum size limit regulations for controlling short-term harvest in recreational fisheries. Fisheries Management and Ecology **20**:258-267.

Venturelli, P. A., C. A. Murphy, B. J. Shuter, T. A. Johnston, P. J. van Coeverden de Groot, P. T. Boag, J. M. Casselman, R. Montgomerie, M. D. Wiegand, and W. C. Leggett. 2010. Maternal influences on population dynamics: evidence from an exploited freshwater fish. Ecology **91**:2003-2012.

Ward, H. G. M., P. J. Askey, and J. R. Post. 2013. A mechanistic understanding of hyperstability in catch per unit effort and density-dependent catchability in a multistock recreational fishery. Canadian Journal of Fisheries and Aquatic Sciences **70**:1542-1550.

Wilberg, M. J. 2009. Estimation of recreational bag limit noncompliance using contact creel survey data. Fisheries Research **99**:239-243.

Wilde, G. R. 1997. Largemouth bass fishery responses to length limits. Fisheries **22**:14-23.

Wilen, J. E., M. D. Smith, D. Lockwood, and L. W. Botsford. 2002. Avoiding surprises: incorporating fisherman behavior into management models. Bulletin of Marine Science **70**:553-575.

Winemiller, K. O. 2005. Life history strategies, population regulation, and implications for fisheries management. Canadian Journal of Fisheries and Aquatic Sciences **62**:872-885.

Woodward, R. T., and W. L. Griffin. 2003. Size and bag limits in recreational fisheries: theoretical and empirical analysis. Marine Resource Economics **18**:239-262.

Wootton, R. J. 1984. Introduction: strategies and tactics in fish reproduction. Pages 1-12 *in* G. W. Poots and R. J. Wootton, editors. Fish reproduction: strategies and tactics. Academic Press, London.

Zhou, S., A. D. M. Smith, A. E. Punt, A. J. Richardson, M. Gibbs, E. A. Fulton, S. Pascoe, C. Bulman, P. Bayliss, and K. Sainsbury. 2010. Ecosystem-based fisheries management requires a change to the selective fishing philosophy. Proceedings of the National Academy of Sciences **107**:9485-9489.

DECLARATION OF AUTHORSHIP

I do hereby solemnly declare that I have completed the preceding PhD thesis independently, and have not used any other sources or aids apart from those listed.

Hiermit erkläre ich, die vorliegende Dissertation selbstständig verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt zu haben.

05.03.2014

_____

Fiona Johnston

APPENDICES

Paper I

I

Johnston, F.D., R. Arlinghaus, J. Stelfox, and J. R. Post. 2011. Decline in angler use despite increased catch rates: anglers' response to the implementation of a total catch-and-release regulation. Fisheries Research. 110(1): 189-197.

Fisheries Research 110 (2011) 189–197

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Decline in angler use despite increased catch rates: Anglers' response to the implementation of a total catch-and-release regulation

Fiona D. Johnston[a,b,*], Robert Arlinghaus[b,c], Jim Stelfox[d], John R. Post[a]

[a] Department of Biological Sciences, University of Calgary, 2500 University Dr. N.W. Calgary, AB, Canada T2N 1N4
[b] Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany
[c] Inland Fisheries Management Laboratory, Department for Crop and Animal Sciences, Faculty of Agriculture and Horticulture, Humboldt-University of Berlin, Philippstrasse 13, Haus 7, 10115 Berlin, Germany
[d] Fish and Wildlife Division, Alberta Sustainable Resource Development, Provincial Building, 213 - 1 Street West, Cochrane, AB, Canada T4C 1B4

ARTICLE INFO

Article history:
Received 14 December 2010
Received in revised form 6 April 2011
Accepted 6 April 2011

Keywords:
Recreational angling
Fisheries management
Catch-and-release regulation
Fishery quality
Angler behaviour

ABSTRACT

A mandatory total catch-and-release regulation and a bait ban were implemented on Lower Kananaskis Lake, Canada, due to the drastic decline of the native bull trout (*Salvelinus confluentus*) population. In the decade following harvest-regulation changes, the adult bull trout population experienced a 28-fold increase in abundance. Two roving creel surveys of winter ice-anglers, the first conducted just prior to the regulation changes (1992) and the second 10 years later (2002), were used to compare catch rates, the size structure of fish caught, and angler effort before and after the bull trout population rebuilt. Supplementary information from voluntary creel cards (1996–2003) was used to evaluate temporal trends in summer catch-related fishery attributes as the fish population recovered. Winter catch rates were three-fold and 12-fold higher in 2002 than in 1992, for all bull trout and large (>50 cm) bull trout, respectively. The proportion of large fish in the catch also increased. Voluntary creel card information suggested summer catch rates and the frequency of large fish in the catch both increased as the population rebuilt. However, despite the increase in fishing "quality", angler numbers were three- to 10-fold lower in 2002 than 1992, indicating reduced utilization of the fishery. We speculate that harvest-oriented anglers were displaced from Lower Kananaskis Lake because of restrictive regulations. Our study shows anglers are not necessarily attracted to high-catch-rate fisheries, suggesting angler behaviour is complex and not driven by catch rates alone. Thus, to meet management objectives, understanding angler effort responses to regulatory changes is fundamentally important.

1. Introduction

One of the main objectives of recreational fisheries management is to establish regulations that prevent overexploitation of self-sustaining fisheries (Radomski et al., 2001; Lewin et al., 2006). Yet, recreational fisheries managers are also concerned with providing attractive fishing experiences for the angling public (Radomski et al., 2001; Cox and Walters, 2002; Peterson and Evans, 2003). Catch aspects play a paramount role in determining angler satisfaction (Arlinghaus, 2006; Hutt and Bettoli, 2007; Arlinghaus et al., 2008a). However, the importance attached to catch-related aspects (e.g., catch rates, abundance of trophy fish) versus non-catch-related aspects (e.g., aesthetic appeal, facilities or water quality) of the fishing experience varies among anglers (Hahn, 1991; Aas et al., 2000; Hunt, 2005). This will affect how different types of anglers perceive and respond to modifications of harvest regulations. For example, the implementation of restrictive harvest regulations has been found to reduce fishing effort by some harvest-oriented anglers (Cox et al., 2002; Beard et al., 2003; Fayram and Schmalz, 2006), likely because they prefer regulations that do not constrain fish harvest (Aas et al., 2000). Thus, harvest regulations (e.g., bag limits, size limits, bait bans) in addition to catch-related and non-catch-related (e.g., proximity to residence) attributes of the fishing experience are all important determinants of angler-effort dynamics (e.g., Cox et al., 2002; Beard et al., 2003). However, behavioural responses of recreational anglers to regulation changes are rarely studied (Metcalf et al., 2010), despite their implications for management (Metcalf et al., 2010; Johnston et al., 2010).

In overexploited populations, one regulatory option for controlling angling mortality is to establish mandatory total catch-and-release regulations. It is argued that allowing such zero-harvest fishing on declining or threatened populations reduces the impacts on the fish stock, while preserving the angling experience and its associated social and economic benefits (Arlinghaus

* Corresponding author at: Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany.
E-mail address: johnston@igb-berlin.de (F.D. Johnston).

0165-7836/$ – see front matter © 2011 Elsevier B.V. All rights reserved.
doi:10.1016/j.fishres.2011.04.006

et al., 2007). However, catch-and-release inevitably results in some unintended hooking mortality (i.e., all forms of non-harvest-related fishing mortality), and sub-lethal impacts that potentially affect fitness (Arlinghaus et al., 2007), although additional regulations such as bait bans may help reduce rates of hooking mortality or injury (Arlinghaus et al., 2008b). Nevertheless, if angling effort or hooking mortality is high enough, zero-harvest policies can still result in undesirable cumulative impacts that accelerate population decline or limit the rate of, or potential for, population recovery (Post et al., 2003; Bartholomew and Bohnsack, 2005; Coggins et al., 2007). Such cumulative impacts are most likely to occur in fish populations with life-history characteristics that make them particularly vulnerable to overexploitation (e.g., slow-growing, late-maturing, high catchability), such as bull trout (*Salvelinus confluentus*) (Post et al., 2003). Furthermore, any increases in stock size that result from regulation changes may be countered by corresponding increases in fishing effort, yielding a "success breeds failure pathology" (Cox and Walters, 2002). Alternatively, as suggested above, the implementation of bait bans or zero-harvest regulations may be unattractive to some anglers who prefer to use organic bait and keep fish, which in turn may reduce angler effort (e.g., Beard et al., 2003). However, given the lack of dedicated studies on angler-effort dynamics, no general predictions about angler responses to changes in regulatory policies and associated fishery attributes (e.g., catch rates, size of catch) are possible. Furthermore, because such responses are probably highly dependent on the specific qualities offered by target species (e.g., consumptive value), substitute-species availability, and local angler customs and culture (Dorow et al., 2010), species- and regional-specific studies on angler-effort dynamics are likely required.

Fishing regulations for bull trout throughout their native range have become increasingly restrictive and widely implemented over the past three decades (e.g., High et al., 2008; Rodtka, 2009), due to concerns about the species' decline in both abundance and spatial distribution (Rodtka, 2009). The bull trout population in Lower Kananaskis Lake, Alberta, Canada, was no exception, as it declined severely from the mid-1950s to the early 1990s, primarily due to overharvest by anglers (Stelfox, 1997). To mitigate bull trout declines in Lower Kananaskis Lake, a total catch-and-release regulation and a bait ban were implemented in 1992. A population time-series, derived from a monitoring study of tagged adult spawners, indicated these regulation changes facilitated the rapid recovery (28-fold increase in adult abundance) of the bull trout population over the next decade (1992–2002) (Johnston et al., 2007). Information from this time-series suggested that the maximum possible annual mortality rate for adult bull trout declined from 48% for the 1991–1992 period (autumn to autumn the next year), the year in which the regulation change occurred, to 5% for the 1992–1993 period, the year after the harvest-regulation changes (Stelfox, 1997). Given the positive response of the bull trout population to the implementation of restrictive regulations, it is inferred that the recovery of the bull trout population was strongly related to a reduction in fishing mortality.

The objective of our study was to determine the corresponding changes that occurred in the fishery as the bull trout population in Lower Kananaskis Lake rebuilt from its severely overexploited state. It is often assumed that angler catch rates are positively related to fish abundance (e.g., Beard et al., 2003; Cox et al., 2003; Post et al., 2003), but this is often not validated. The bull trout fishery on Lower Kananaskis Lake provided an opportunity to evaluate how regulation changes influenced catch-related fishery quality and angler behaviour, because information was available from two winter creel surveys – one conducted just prior to regulation changes in 1992 and one conducted a decade later in 2002, after the bull trout population had rebuilt. Furthermore, angler catch data for the summer months was also available from voluntary creel cards

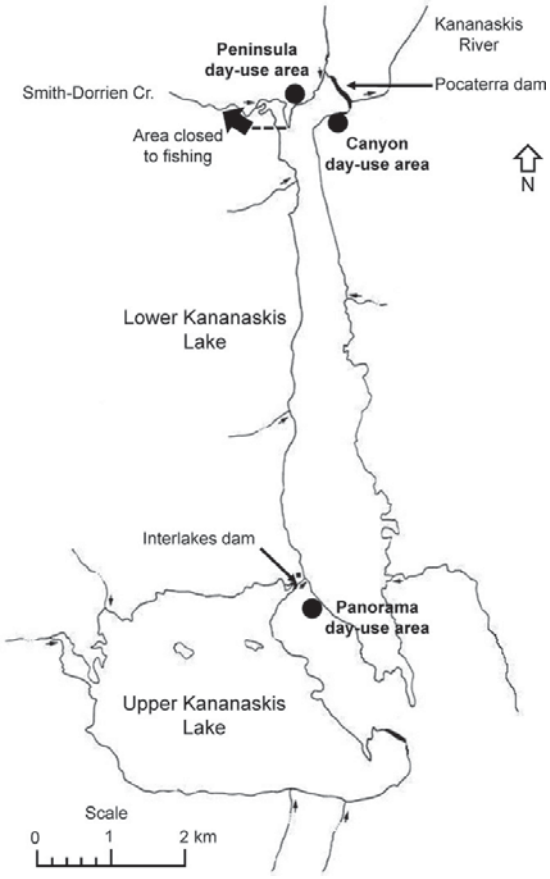


Fig. 1. Angler access points on Lower Kananaskis Lake, Alberta, Canada.

(1996–2003). These data provided information on temporal trends in anglers' catches, allowing us to assess if catch-related fishery quality consistently changed as the bull trout population rebuilt. Using these data, we investigated the following questions; (*i*) did the catch-related attributes of the fishery change as the bull trout population recovered? and (*ii*), how did angler utilization of the fishery change in response to any corresponding changes in catch-related fishery quality? It was expected that as stock abundance levels increased that catch rates and the size of bull trout caught would also increase, and that this increase in catch-related fishery quality would attract greater angler use.

2. Materials and methods

2.1. Study area

The study area, Lower Kananaskis Lake, is a 646 ha hydroelectric reservoir located in Peter Lougheed Provincial park, Alberta, Canada (50°38′59″N–115°7′59″W; Fig. 1). It is usually ice covered from early December until early May (Stelfox, 1997). The recreationally valuable fish in the lake include native bull trout, native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*), and nonnative rainbow trout (*Oncorhynchus mykiss*). Upper Kananaskis Lake (Fig. 1) – located 1 km upstream of Lower Kananaskis Lake – only contained rainbow trout and cutthroat trout until 2001, when bull trout

were stocked. Rainbow trout, were regularly stocked into Lower Kananaskis Lake from 1959 to 1988 (Stelfox, 1997), but this was discontinued during the 1990s to facilitate the recovery of the bull trout population by reducing fishing pressure. In Upper Kananaskis Lake, rainbow trout not only continued to be stocked after 1988, but also from 1992 until 2002 the stocked rainbow trout were larger, catchable-sized fish, rather than the smaller rainbow trout stocked prior to 1992. However, any downstream movement of fish via the turbine of the Interlakes dam (Fig. 1) is limited (Stelfox, 1997).

Province-wide prior to 1992, anglers were able to harvest two bull trout per day over 40-cm. However, due to the substantial decline of bull trout in Lower Kananaskis Lake, special angling regulations were implemented for this lake on 1 April 1992 (Stelfox, 1997). The northwest bay of the lake and the spawning creek – Smith-Dorrien Creek – were permanently closed to fishing (Fig. 1). On the rest of the lake, a ban on organic bait and a total catch-and-release regulation for bull trout were implemented. In 1995, the zero-harvest regulation for bull trout was implemented province-wide. For all other trout species in the Upper and Lower Kananaskis Lakes, the regulations during the study period were five fish per day of any size.

2.2. Angler surveys

To determine if the catch-related fishery attributes increased as the bull trout population recovered, we compared how winter catch rates and the size distribution of the catch differed between the two winter creel surveys, pre and post overexploitation. We also used voluntary creel card data to determine if summer catch rates and the size distribution of the catch were related to the bull trout population's recovery from a severely overexploited state. To determine if angler utilization of the fishery changed with changes in catch-related fishery quality, we examined angler effort differences pre and post regulation change using the winter creel data.

2.2.1. Winter roving creel surveys

The first roving creel survey was conducted between December 1991 and March 1992, and the second between January 2002 and mid-June 2002. Here, only data from the months of January to March were used to have equivalent periods for comparison. Sampling was stratified according to day type, weekend days (and holidays) and weekdays, to reduce the variance associated with survey estimates (Pollock et al., 1994). More weekend days were surveyed (72%) than weekdays (19%), because weekends were expected to have the highest angling activity (Malvestuto, 1996) (Table 1). An attempt was made to sample one to two days during the work week and most weekends.

During the creel survey, the two main access points for ice anglers on Lower Kananaskis Lake – Canyon and Panorama day-use areas (Fig. 1) – were patrolled. The few anglers that accessed the lake from other points were visible from these locations and were also surveyed. Angler counts were made on arrival at a location and all anglers were surveyed. Because total counts required less than an hour to complete, they were treated as instantaneous counts as outlined in Pollock et al. (1994). In 1992, one survey was conducted per survey day by Fish and Wildlife officers (subject to their availability), except on 12 and 18 January, when officers were present the entire day. In 2002, the lake was surveyed twice per day (a.m. between 09:30 and 13:00, mean 11:00; and p.m. between 13:30 and 17:00, mean 15:30). Because so few anglers were present in 2002, we could also identify groups that were present during both the morning and afternoon counts (i.e., identify repeat contacts) to obtain an estimate of total daily angler number. In both years, anglers provided the hours they had fished (incomplete trips), and the number and size of fish caught and released during this period (based on 10-cm size categories). In 2002, information was only collected on the angling group level, not for individual anglers (as was done in 1992). Thus, group information (e.g., catch rate = total group catch/total group effort) from 1992 and 2002 was used in all calculations.

2.2.2. Voluntary creel cards

In addition to the two roving creel surveys, on 24 July 1995, two voluntary creel survey boxes were installed around Lower Kananaskis Lake, at the Panorama and Canyon day-use areas (Fig. 1). On 28 June 1996, a third creel survey box was installed at the Peninsula day-use area, and all three have been maintained since that time. Creel cards were filled in voluntarily, and provided angler information on hours fished (completed trips), number of fish caught by species, and size distribution (based on 10-cm size categories) of the catch. However, sample sizes from the winter months were generally small (often <5 cards). Therefore, only voluntary creel card information from May to July for the years 1996–2003 was used (sample size = 45, 50, 148, 52, 78, 39, 59, and 59, for 1996, 1997, 1998, 1999, 2000, 2001, 2002, and 2003, respectively), because these months represent the ice-free period prior to when bull trout begin their fall spawning migration out of Lower Kananaskis Lake into Smith-Dorrien Creek in August (Stelfox, 1997). Data from 1995 were excluded because the creel boxes were only installed at the end of July. Voluntary returns are subject to biases (Pollock et al., 1994), but we assume a systematic bias such that temporal analyses seem warranted.

2.3. Analyses

The following data were available for our analyses: (*i*) two point estimates of winter (January to March) catch rates, size distribution of the catch, and effort, pre and post recovery, from the winter creel surveys, (*ii*) a time-series of summer (May to July) catch rates and size distribution of the catch from the voluntary creel cards, and (*iii*) a fishery-independent time-series of adult bull trout abundance estimates from a monitoring study of tagged bull trout spawners (see Johnston et al., 2007).

2.3.1. Winter effort and catch rates

Angler-count data were used to determine how angler use of Lower Kananaskis Lake differed between 1992 and 2002. Daily angler number was estimated from the single count from 1992 and the average of the two angler counts from 2002. Daily estimates, including survey days when no anglers were present, were then used to calculate mean daily angler number for each year and day-type strata separately. For comparative purposes, mean daily angler number was also calculated using daily estimates of total angler number from 2002 (i.e., accounting for angler groups encountered in both the morning and afternoon) rather than the average of the two instantaneous counts (see Section 4.1).

To determine if catch rates between 1992 and 2002 differed, we compared mean catch rates $\bar{C}$ calculated using the mean-of-ratios method, which is appropriate for incomplete trip data in roving creel surveys (Pollock et al., 1994, 1997; Jones et al., 1995),

$$\bar{C} = \frac{1}{N}\sum_{i=1}^{N}\bar{C}_i, \quad \text{where} \quad \bar{C}_i = \frac{1}{n_i}\sum_{j=1}^{n_i}\left(\frac{C_{ij}}{E_{ij}}\right), \tag{1}$$

where N is the number of days sampled, $\bar{C}_i$ is the average group catch-per-unit-effort from all groups fishing on a given day i, n_i is the number of groups sampled on a given day i, C_{ij} is the number of fish caught by group j on day i, and E_{ij} is the number of hours fished by group j on day i. Mean catch rates for all trout species, bull trout, and adult (>50 cm) bull trout were calculated for each year and day-type strata. We assumed that fish >50 cm were adults,

Table 1
Summary of angler survey dates on Lower Kananaskis Lake. Values in parentheses indicate the number of days anglers were present.

Year	Day type	Month			Total	Total possible
		January	February	March		
1992	Weekend	7	6	2	15 (13)	28
	Weekday	3	4	1	8 (8)	63
2002	Weekend	8	8	10	26 (16)	29
	Weekday	8	4	3	15 (2)	61
Total		26	22	16	64 (39)	
Total possible		62	57	62		181

which is warranted for Lower Kananaskis Lake bull trout (Johnston and Post, 2009). Catch rates of all trout species were calculated, because of their potential influence on angler effort if anglers were targeting all trout species rather than bull trout alone. In winter catch rate calculations, we only included days when anglers fished, and excluded angler groups which fished <0.5 h, as recommended by Pollock et al. (1994). Catch data were highly skewed and zero inflated, which is common (Jones et al., 1995; Hoyle and Cameron, 2003), as were the number of anglers fishing per day. For this reason, 95% confidence intervals around the means were calculated using a non-parametric bootstrapping technique with 10,000 iterations. The bootstrap-*t* method ("bootstrap" R 2.11.0) was used because it has been found to be the least biased when estimating catch rates from recreational fishing surveys (Hoyle and Cameron, 2003).

To determine if mean daily angler numbers and mean catch rates differed between the years, two-sample randomization tests were used. Randomization tests are suitable for analyzing non-normal data which violate assumptions of standard parametric tests or, in the case of many tied values, make non-parametric tests less suitable (Manly, 1997). Data from both 1992 and 2002 were randomly assigning a year in proportion to the sample size from each year. This was done 10,000 times. For each iteration, mean daily angler number or mean catch rate was calculated for both years and the difference between the means was estimated. The proportion of iterations in which means differed by greater than (or less than) the difference in means from the original data determined the probability that the original difference in means was due to chance alone (Manly, 1997).

2.3.2. Summer catch rates

Mean catch rates from voluntary creel information were calculated using a ratio-of-means method, which is appropriate for complete trip information (Pollock et al., 1994; Jones et al., 1995),

$$\bar{C} = \frac{1}{N}\sum_{i=1}^{N}\bar{C}_i, \quad \text{where} \quad \bar{C}_i = \sum_{j=1}^{n_i} C_{ij} / \sum_{j=1}^{n_i} E_{ij}. \tag{2}$$

Mean catch rates were calculated for bull trout and adult (>50 cm) bull trout. To determine if summer catch rates increased with adult bull trout density *V*, catch rate was modeled as a nonlinear function of adult bull trout density,

$$\bar{C} = \alpha V^{\beta}, \tag{3}$$

using a linear regression fit to log-transformed data, as outlined in Hansen et al. (2000). β represents the degree of curvature, and if different from one suggests that catchability (the proportion of fish caught per unit fishing effort) is density dependent, while α estimates catchability when there is no density dependence (Hansen et al., 2000). Adult bull trout density estimates, independent from the angler surveys, were obtained from a study conducted from 1991 to 2002 that monitored tagged bull trout spawners (Johnston et al., 2007). Data from 2003 were excluded from this analysis because no adult bull trout abundance estimate was available.

2.3.3. Size distribution of the catch

To determine if the size distribution of fish caught during the winter creel survey differed across the five size classes (20–30 cm, 30–40 cm, 40–50 cm, 50–60 cm, >60 cm) between 1992 and 2002, Fisher's exact test was used ("fisher.test" R 2.11.0) because of the low expected frequency of some of the size classes (Crawley, 2007). Five post hoc tests of equal proportions were used to examine which size classes differed between years ("prop.test" R 2.11.0). *p*-values were adjusted for multiple comparisons using the Holm method (Holm, 1979).

Voluntary creel information on the size distribution of the catch was also examined for temporal trends over the period from 1996 to 2003. A generalized linear model ("glm" R 2.11.0) was used to determine if year or adult bull trout density affected the proportion of bull trout >50 cm in the catch. A quasibinomial distribution rather than a binomial distribution was used in the model because of overdispersion of the data (Crawley, 2007). Data from 2003 were included in the analysis of temporal trends, but excluded from the analysis of density trends because abundance estimates were not available for 2003.

All analyses were implemented in R 2.11.0 (R Development Core Team, 2010), and tests with $p < 0.05$ were considered significant.

3. Results

3.1. Winter catch rates

Compared to 1992, mean winter catch rates of bull trout were significantly higher (three- and nine-fold higher, randomization test, one-tailed: $p = 0.0018$ and $p = 0.0223$, for weekends/holidays and weekdays, respectively; Fig. 2) in 2002, as were mean winter catch rates of bull trout >50 cm (18- and 12-fold higher, randomization test, one-tailed: $p = 0.0017$ and $p = 0.0218$, for weekends/holidays and weekdays, respectively; Fig. 2). In 1992, 71% (27/38) of the bull trout caught were harvested, whereas in 2002, none of the 127 bull trout caught were harvested (assuming full compliance with regulations). Four rainbow trout were caught on weekends in 1992, but weekend winter catch rates including all trout species and bull trout alone did not differ significantly between 1992 and 2002 (randomization test, two-tailed: $p = 0.9947$). No non-bull-trout species were caught in 2002, or on weekdays in 1992.

3.2. Summer catch rates

Mean summer catch rates of bull trout $\bar{C}$ and adult (>50 cm) bull trout $\bar{C}_{>50}$ obtained from the voluntary creel cards increased with increased adult bull trout density (from Johnston et al. 2007) ($R^2 = 0.70$, $p = 0.0183$ and $R^2 = 0.73$, $p = 0.0141$ for all bull trout and adult bull trout, respectively; Fig. 3). As adult bull trout density increased 2.3-fold from 1996 to 2000, summer catch rates increased by 3.1 and 2.9 times for all bull trout and bull trout >50 cm, respectively (Fig. 3). Catch rates were linearly related to adult bull trout density, $\bar{C} = 0.192\,V$ and $\bar{C}_{>50} = 0.105\,V$, because β was not

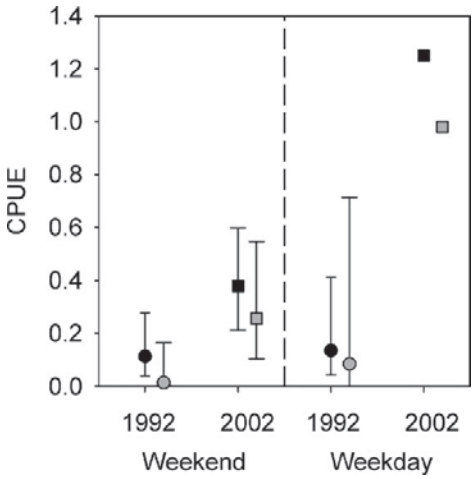


Fig. 2. The catch-per-unit-effort (CPUE) of bull trout of all sizes (black symbols) and bull trout >50 cm (gray symbols) during the winter creel surveys in 1992 and 2002, stratified by day type (weekday or weekend/holiday). Error bars represent 95% confidence intervals estimated using the bootstrap-*t* method, except in 2002 weekdays due low sample size (2 days). Sample sizes are reported in Table 1.

significantly different from one ($p = 0.7388$ and $p = 0.5092$ for all bull trout and bull trout >50 cm, respectively), i.e., catchability was not found to be density dependent.

3.3. Winter and summer catch size distribution

Size structure of the bull trout caught by anglers differed significantly between the 1992 and 2002 winter creel surveys (Fisher's exact test: two-tailed $p = 2.94 \times 10^{-7}$; Fig. 4). The proportions of small bull trout in the 30–40 cm and 40–50 cm size classes were significantly greater in 1992 than 2002, and the proportion of large fish in the >60 cm size class was significantly greater in 2002 than 1992 (test of equal proportions: $p_{adj} = 0.1581$, $p_{adj} = 0.0067$, $p_{adj} = 0.0067$, $p_{adj} = 0.1581$, $p_{adj} = 0.0059$, for the 20–30 cm, 30–40 cm, 40–50 cm, 50–60 cm, and >60 cm size classes, respectively; Fig. 4). In 1992, 82% of the bull trout caught (31/38) were over the legal size limit of 40 cm, and 87% (27/31) of these legal-sized bull trout were harvested. Information obtained from the voluntary creel cards on the size of bull trout caught (530 fish, 1996–2003) also demonstrated a significant increase in the proportion of adult (>50 cm) fish in the catch over time (i.e., with year, GLM: two-tailed $p = 0.0266$; Fig. 5); however this increase was not significantly related to adult bull trout density (GLM: two-tailed $p = 0.269$).

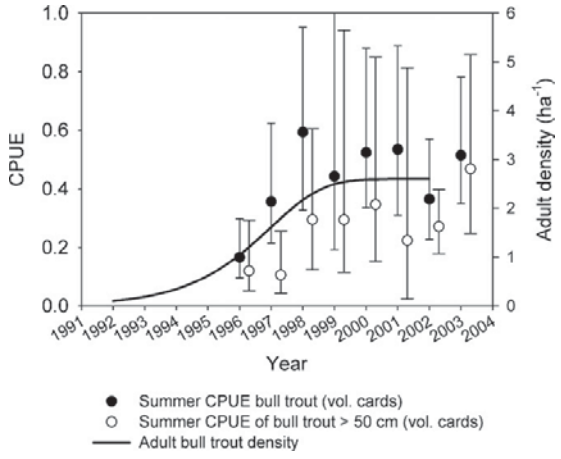


Fig. 3. Mean summer (May to July) catch-per-unit-effort (CPUE) of all bull trout and bull trout >50 cm obtained from voluntary creel cards (sample days = 32, 28, 38, 37, 41, 17, 22, and 26, for 1996, 1997, 1998, 1999, 2000, 2001, 2002, 2003, respectively) and adult bull trout density from Johnston et al. (2007). Error bars represent 95% confidence intervals estimated using the bootstrap-*t* method.

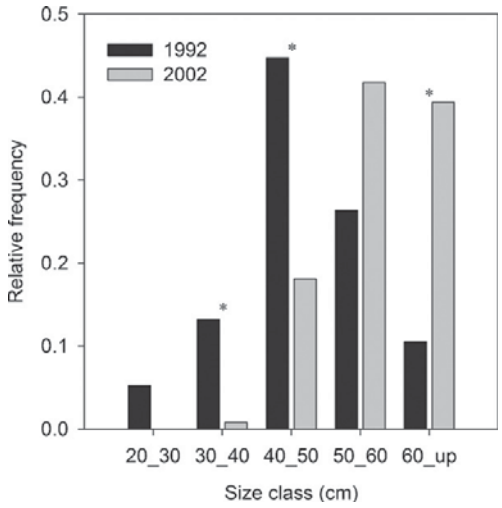


Fig. 4. The size structure of the bull trout, as determined by relative frequency, caught by angling during the winter creel surveys in 1992 (38 fish) and 2002 (127 fish). The stars indicate which proportions were significantly different ($\alpha = 0.05$) based on post hoc tests of equal proportions.

3.4. Angler effort

Despite the higher mean catch rates and larger size of bull trout caught in 2002 relative to 1992, significantly fewer anglers (10- to 32-fold less, randomization test, two-tailed: $p \leq 0.0001$ and $p \leq 0.0001$ for weekends/holidays and weekdays, respectively; Table 2) were present on a given day in 2002 than in 1992

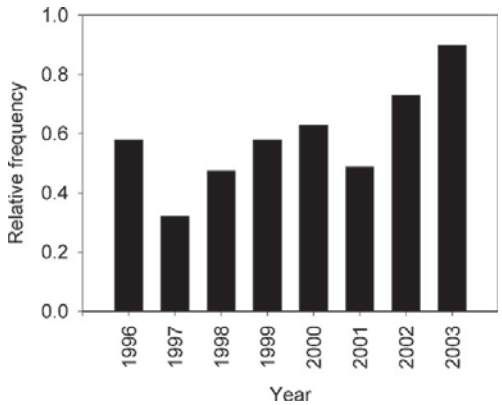


Fig. 5. The relative frequency of bull trout >50 cm caught by summer angling from 1996 to 2003 according to information from voluntary creel cards (sample size = 45, 50, 148, 52, 78, 39, 59, and 59 fish, for 1996, 1997, 1998, 1999, 2000, 2001, 2002, and 2003, respectively).

Table 2
Mean daily angler number present during the winter creel surveys in 1992 and 2002. Values for 2002 were calculated in two ways; using the mean of the two counts of angler number from each day, and using the estimate of total anglers present on each day. Sample sizes are total values reported in Table 1 Values in parentheses represent the 95% confidence intervals estimated using the bootstrap-*t* method.

Year	Day type	
	Weekend	Weekday
1992	6.5 (3.7, 9.8)	3.3 (2.3, 4.0)
2002 – mean of two counts	0.7 (0.5, 0.9)	0.1 (0.0, 0.3)
2002 – total anglers present	2.3 (1.2, 4.0)	0.4 (0.0, 1.1)

(123 anglers and 67 anglers were surveyed in 1992 and 2002, respectively). The same trends were found for total daily angler number from 2002 (i.e., when we account for anglers present in the morning and afternoon in 2002), when three- to eight-fold more anglers were present in 1992 relative to 2002; (randomization test, two-tailed: $p = 0.0037$ and $p = 0.0004$ for weekends/holidays and weekdays, respectively; Table 2).

4. Discussion

With the implementation of a total catch-and-release regulation and organic bait ban, the bull trout population in Lower Kananaskis Lake recovered from its previously overexploited state, exhibiting a 28-fold increase in adult abundance over the period of a decade (1992–2002) (Johnston et al., 2007). Our study examined how the catch-related quality of the fishery and the number of anglers it attracted changed with the substantial recovery of the bull trout population. Results from our study revealed that catch-related fishery quality (catch rate and size of bull trout caught) increased as the fish population rebuilt, yet angler utilization of the fishery decreased substantially. Our findings suggest that the attractiveness of the fishery declined, likely because catch rates did not constitute the sole determinant of fishery quality. Instead, it is likely that anglers fishing in Lower Kananaskis Lake during the 1992 winter fishery valued fish harvest, thus in 2002 the restrictive harvest regulations resulted in reduced use by these anglers.

Comparison of two winter creel surveys, the first carried out in 1992 just prior to regulation changes and the second conducted a decade later (2002), demonstrated that winter catch rates were higher – at least three-fold for all bull trout and at least 12-fold for adult (>50 cm) bull trout – after population recovery. In addition, summer catch rates of bull trout from voluntary creel cards (1996–2003) were found to increase with fish density. It is often assumed that there is a positive relationship between catch rates and fish abundance (e.g., Beard et al., 2003; Cox et al., 2003; Post et al., 2003), and our results validate this assumption for bull trout. Although not directly comparable, in combination our results suggest that angler catch rates can increase substantially after the implementation of restrictive harvest regulations. Furthermore, the temporal increase in summer catch rates suggests that cues of improving catch rates were consistently signaled to summer anglers, which is important as previous experiences likely influence anglers' fishing decisions (Adamowicz, 1994).

Not only catch rates but also the size of bull trout caught increased with the bull trout population's recovery. Indeed, the fraction of large, trophy-sized (e.g., >60 cm) bull trout in the winter catch was substantially higher in 2002 than 1992, demonstrating the degree to which the population was truncated by harvest prior to regulation changes. Temporal increases in the proportion of bull trout >50 cm in the summer catch were also found, as the size structure of the population rebuilt. Evidence for strong size truncation of the population is not a surprising result, given that anglers harvested 91% of legal-sized (≥40 cm) bull trout that were caught during the 1991–1992 winter fishery (Stelfox, 1995). Indeed, maximum annual mortality of adult bull trout from 1991 to 1992 was 48%, most of which was likely due to angler harvest during the winter ice-fishing season (Stelfox, 1997). Thus, similar to other recreational fisheries (see review in Lewin et al., 2006), exploitation rates of bull trout in Lower Kananaskis Lake were substantial, and the annual exploitation rate would likely have been higher for the 1991–1992 period had the zero-harvest regulation not been implemented on 1 April 1992 (Stelfox, 1997).

Given that both catch rate and fish size are important determinants of anglers' fishing participation decisions (Aas et al., 2000; Hunt, 2005), increases in these catch-related attributes are often expected to attract effort to a fishery (Cox and Walters, 2002; Post et al., 2003). Indeed, this was reported in several empirical studies (e.g., Anderson and Nehring, 1984; Novinger, 1987; Cornelius and Margenau, 1999; Newman and Hoff, 2000). However, other studies have found that total catch-and-release regulations or more stringent size or daily bag limits may result in reduced angler effort despite similar or increased catch rates (e.g., Muoneke, 1994; Almodóvar and Nicola, 1998; Boxrucker, 2002; Hurley and Jackson, 2002; Parker et al., 2007). Similarly, restrictive fly-only regulations that prohibited the use of organic bait were also been found to reduce angling pressure on a trout stream (Shetter and Alexander, 1962). On Lower Kananaskis Lake, we observed a significant decrease in angler use (minimum three- to 10-fold lower in 2002 than 1992) after the implementation of total catch-and-release regulations and the bait ban, despite the elevated catch rates (three-fold higher in 2002 than 1992), and the increased dominance of large fish in the catch. This finding clearly illustrates that factors other than catch-related attributes alone are important for determining angler effort.

Reasons for reduced angler effort despite increases in catch rates and the capture of large fish likely relates to what attributes anglers jointly consider when assessing the quality of a fishery. Indeed, earlier research has emphasized that angler effort responses are determined by multiple catch and non-catch related factors, including angling regulations (Aas et al., 2000; Oh et al., 2005; Hunt, 2005), and are not simply linked to fishing successes alone (Johnson and Carpenter, 1994; Hunt, 2005; Post et al., 2008; Johnston et al., 2010; Hunt et al., in press). In particular, harvest regulations may alter the attractiveness of a fishery if they are perceived to constrain anglers' opportunities to harvest fish (Radomski and Goeman, 1996; Dorr et al., 2002; Cox et al., 2002), or if they alter anglers' expectations about the fishery (Fayram et al., 2006; Cook et al., 2001; Beard et al., 2003). For example, Beard et al. (2003) found that, despite having higher catch rates, walleye (*Sander vitreus*) anglers fished less on lakes with lower bag limits because anglers assumed that lower bag limits indicated poor quality fisheries. In the case of Lower Kananaskis Lake, it is hypothesized that the significantly lower angler effort in 2002 than 1992 was due, in part, to some anglers choosing not to fish on this lake in 2002 because the zero-harvest regulation and bait ban limited their ability to harvest fish. Thus, equating catch rates alone with fishery "quality" and in turn angler-effort responses, as has sometimes been assumed in fisheries models (e.g., Cox et al., 2003; Post et al., 2003), might be overly simplistic, and could result in misleading predictions about the numerical response of anglers to regulatory or other changes in the fishery (Johnston et al., 2010; Hunt et al., in press). However, by altering angler behaviour independent of catch (Beard et al., 2003; Fayram et al., 2006), stringent harvest regulations may also indirectly control harvest (Cox et al., 2002). Thus, while the zero-harvest regulations directly prohibited bull trout harvest in Lower Kananaskis Lake, the reduced angler use in response to restrictive regulations likely also aided the recovery of the bull trout population by minimizing cumulative hooking mortality. If the effort response of the angling public had been different and total angling

effort had increased over time, it is possible hooking mortality alone could have been sufficient to impede the recovery of the bull trout fishery (Post et al., 2003).

Regulation changes on Lower Kananaskis Lake did not deter all anglers, however, supporting suggestions that not all anglers will respond in a similar manner to the same angling regulations (Quinn, 1992; Jacobson, 1996; Aas et al., 2000; Beard et al., 2003). Numerous studies have shown that some anglers are less harvest-oriented and more interested in catching trophy-sized fish (Bryan, 1977; Fisher, 1997; Arlinghaus, 2007), and that these anglers often favour restrictive harvest regulations (Chipman and Helfrich, 1988; Gigliotti and Peyton, 1993; Hutt and Bettoli, 2007). We thus hypothesize that the anglers that fished on Lower Kananaskis Lake in 2002 were primarily less consumptively oriented anglers who were more interested in non-harvest aspects of the fishery (e.g., trophy-sized bull trout) than 1992 anglers. Anecdotal support for this hypothesis originates from conversations with some anglers in 2002, which revealed their desire to maintain the total catch-and-release regulation or to introduce very limited harvest (pers. obs., F.D. Johnston). Overall, our results add to the growing number of studies (e.g., Beard et al., 2003; Johnson and Carpenter, 1994) which suggest that understanding the response of the angler population to changes in regulation is not straight forward, and strongly depends on the preferences of the angling public and the relative frequency of different angler types in the population (Beard et al., 2003; Johnston et al., 2010). Human dimensions data is required to better understand the composition of the regional angler population and how different angler types in this population will respond to the implementation of restrictive harvest policies.

4.1. Limitations and alternative hypotheses

We hypothesize that angler numbers decreased, despite increased catch rates and size of fish caught, primarily because of an aversion by harvest-oriented anglers to restrictive regulations. However, we cannot unambiguously demonstrate that the implementation of a total catch-and-release regulation and bait ban were solely responsible for the change in angler use on Lower Kananaskis Lake. Several other factors could confound this simple explanation. Catch rates of all trout species rather than bull trout alone could have influenced angler effort. However, this is unlikely the reason for lower angler numbers in 2002 than 1992, because catch rates of all trout did not differ among years as few non-bull trout species were caught in either year. Individual fisheries are imbedded in a landscape of alternate fisheries (Lester et al., 2003; Carpenter and Brock, 2004; Post et al., 2008; Hunt et al., in press), and the milieu of management regulations and stocking practices within the landscape may also impact angling effort on a given lake. For example, changes in management (e.g., stocking practices) on other fisheries within the region of interest to Lower Kananaskis Lake anglers could have contributed to the decline in angler numbers on Lower Kananaskis Lake, as stocking practices may alter the attractiveness of a fishery (e.g., Johnson and Carpenter, 1994). Thus, the change to stocking larger, catchable-sized rainbow trout from 1992 to 2002 in Upper Kananaskis Lake where bait was still permitted, in combination with the discontinued stocking of rainbow trout in Lower Kananaskis Lake, could have caused some anglers to redirect their efforts to nearby Upper Kananaskis Lake. Clearly more information on angler effort across the landscape, and on angler motivations and behaviour, is required to properly balance all factors involved in attracting or repelling recreational fishing effort on an individual fishery.

A second possible explanation for our results is that there was a regional decline in angler effort from 1992 to 2002. Indeed, there is evidence that the number of active anglers in Alberta decreased 14% from 1990 to 2000, and similarly the number of hours anglers spent ice-fishing in Alberta decreased 24% (Fisheries and Oceans Canada, 1990, 2000). However, these declines were not nearly as substantial as those observed at Lower Kananaskis Lake. Furthermore, angler effort on a nearby lake, Lake Minnewanka, increased 6% with a 30% increase in catch rates from 1991 to 2000, although harvest rates were similar (Pacas and Hunt, 2004), suggesting that angler effort in the area did not drop off substantially over the study period. Thus, regional angling trends are insufficient to explain the strong declines we observed on Lower Kananaskis Lake.

We also acknowledge some methodological limitations in our study. In particular, we do not have information on the temporal dynamics of angler effort throughout the study period. For example, angler effort may have declined dramatically immediately after the regulations were changed in 1992, and has increased since that time, albeit not to pre-regulation-change levels, as improvements in catch-related aspects of the fishery became known (Fig. 3). Another limitation was that differences between the two winter survey methods required that information was compared on the angler group level rather than the individual angler level for consistency. However, the use of group information is suitable when the purpose is to determine catch and effort in the fishery rather than differences among anglers (Pollock et al., 1994). Voluntary catch cards are also typically biased towards successful anglers (Pollock et al., 1994), and both surveys relied on angler recall of fish size, both of which may have biased catch-related results. However, this is only an issue if the magnitude and direction of the bias differed among years. A further limitation was that the count timing during a day was not randomly selected nor were the days sampled. For this reason we did not try to predict overall effort and catch for the fishery. As with any roving creel survey, it is possible more successful anglers fished longer and thus were more likely intercepted, biasing catch rates high (Pollock et al., 1994). The single count in 1992 also likely resulted in more anglers being missed than occurred in 2002. However, accounting for these biases would only increase the differences we observed between 1992 and 2002, as angler number would be biased low and catch rates high in 1992 relative to 2002. Furthermore, if we compared the higher estimate of daily angler number for 2002 – estimated by identifying groups that fished in both the a.m. and p.m, rather than average daily angler number – to the 1992 estimate of daily angler number, we still found angler effort to be significantly higher in 1992 than 2002 (see results and Table 2). Finally, it should be recognized that the sample sizes from the angler surveys were small, particularly in terms of weekday catch rates (<15% of possible weekdays were sampled). However, over 50% of the possible weekend days were sampled, and despite small sample sizes we found clear differences. Thus, overall we are confident that our results are robust despite the mentioned limitations.

4.2. Conclusions and implications

Our results suggest that the implementation of a total catch-and-release regulation and a bait ban were successful in improving the catch-related attributes (i.e., catch rates and size of fish caught) of the Lower Kananaskis Lake fishery. However, the decline in angler effort by 90%, suggests regulation changes may have impacted some anglers' perceptions about the quality (i.e., reduced harvest potential) of the Lower Kananaskis Lake fishery, deterring them from fishing after restrictive regulations were implemented. Thus, our study shows that it may be overly simplistic to assume that angler use is directly related to catch-related aspects of a fishery alone (e.g., Cox et al., 2003; Post et al., 2003). If anglers are interested in using bait and harvesting fish, they may not take advantage of high catch rates that might result under restrictive regulations, and may become disgruntled (Sullivan, 2003). Indeed, despite a trend towards less harvest-oriented angler behaviour and

voluntary catch-and-release in some fisheries (e.g., Slipke et al., 1998; Simonson and Hewett, 1999; Mosindy and Duffy, 2007; Allen et al., 2008; Myers et al., 2008), anglers in Alberta surveyed in 1990 and 1995 rated the reason "to catch fish to eat" 53% higher than "to catch a trophy fish" in determining their fishing site choice (Fisheries and Oceans Canada, 1990, 1995; not collected in 2000). Where dissatisfied anglers, displaced from fisheries with restricted harvest, might redirect their effort in the fishery landscape will also likely strongly affect the use and exploitation of alternative fisheries in the region (Lester et al., 2003; Carpenter and Brock, 2004; Parkinson et al., 2004; Hunt et al., in press). For example, many of the more harvest-oriented anglers from Lower Kananaskis Lake may have moved to the nearby Upper Kananaskis Lake where harvestable, catchable-sized rainbow trout were stocked and no bait ban was in place. Thus, to manage recreational fisheries in both a biologically and socially sustainable manner, we need to know more about how anglers will respond to changes in both catch (e.g., catch rates, size of catch) and non-catch (e.g., regulations) attributes of fisheries, and how the responses differ among anglers in the community. This requires more directed studies on the influence of fishery attributes, such as regulations, on the temporal and spatial dynamics of anglers in relation to fishery attributes, and how responses differ among different types of anglers. Ignoring angler effort responses can lead to management failures (Johnson and Carpenter, 1994; Radomski et al., 2001; Beard et al., 2003; Post et al., 2003; Fayram and Schmalz, 2006; Johnston et al., 2010), and can have far-reaching impacts on fisheries (Post et al., 2002, 2008; Hunt et al., in press).

Acknowledgements

This study could not have been conducted without the support of the University of Calgary, Alberta Sustainable Resource Development (SRD) – Fish and Wildlife Division, Tourism, Parks and Recreation (TPR) – Parks Division, and the Alberta Conservation Association (ACA). We would like to acknowledge B. Lajeunesse (SRD), K. Fitzsimmons (ACA), M. Fontana (ACA), and J. Wieliczko (ACA) for their assistance in conducting the weekend creel surveys, the Peter Lougheed Conservation Officers (TPR), D. Schley, R. Axani, C. Scotland, A. Rees, D. Hanna, and N. Michalchuk, for conducting the weekday creel surveys, and TPR for providing lodging. Finally, we would like to acknowledge two anonymous reviewers for their constructive comments that helped improve the manuscript clarity. Financial support for this research was in part provided by Challenge Grants in Biodiversity, the ACA, and the Natural Sciences and Engineering Research Council. RA and FJ received additional financial support from the Gottfried-Wilhelm-Leibniz Community through the Adaptfish Project (www.adaptfish.igb-berlin.de) and RA through the German Ministry for Education and Research (BMBF) through the Program for Social-Ecological Research (SOEF) within the Besatzfisch-Project (# 01UU0907, www.besatz-fisch.de).

References

Aas, Ø., Haider, W., Hunt, L., 2000. Angler responses to potential harvest regulations in a Norwegian sport fishery: a conjoint-based choice modeling approach. N. Am. J. Fish. Manage. 20 (4), 940–950.

Adamowicz, W.L., 1994. Habit formation and variety seeking in a discrete choice model of recreational demand. J. Agric. Resour. Econ. 19 (1), 19–31.

Allen, M.S., Walters, C.J., Myers, R., 2008. Temporal trends in largemouth bass mortality, with fishery implications. N. Am. J. Fish. Manage. 28 (2), 418–427.

Almodóvar, A., Nicola, G.G., 1998. Assessment of a brown trout *Salmo trutta* population in the River Gallo (central Spain): angling effects and management implications (Salmonidae). Ital. J. Zool. 65 (Suppl. 1), 539–1539.

Anderson, R.M., Nehring, R.B., 1984. Effects of a catch-and-release regulation on a wild trout population in Colorado and its acceptance by anglers. N. Am. J. Fish. Manage. 4 (3), 257–265.

Arlinghaus, R., 2006. On the apparently striking disconnect between motivation and satisfaction in recreational fishing: the case of catch orientation of German anglers. N. Am. J. Fish. Manage. 26, 592–605.

Arlinghaus, R., 2007. Voluntary catch-and-release can generate conflict within the recreational angling community: a qualitative case study of specialised carp, *Cyprinus carpio*, angling in Germany. Fish. Manage. Ecol. 14 (2), 161–171.

Arlinghaus, R., Cooke, S.J., Lyman, J., Policansky, D., Schwab, A., Suski, C., Sutton, S.G., Thorstad, E.B., 2007. Understanding the complexity of catch-and-release in recreational fishing: an integrative synthesis of global knowledge from historical, ethical, social and biological perspectives. Rev. Fish. Sci. 15, 75–167.

Arlinghaus, R., Bork, M., Fladung, E., 2008a. Understanding the heterogeneity of recreational anglers across an urban-rural gradient in a metropolitan area (Berlin, Germany), with implications for fisheries management. Fish. Res. 92 (1), 53–62.

Arlinghaus, R., Klefoth, T., Kobler, A., Cooke, S.J., 2008b. Size selectivity, injury, handling time, and determinants of initial hooking mortality in recreational angling for northern pike: the influence of type and size of bait. N. Am. J. Fish. Manage. 28 (1), 123–134.

Bartholomew, A., Bohnsack, J., 2005. A review of catch-and-release angling mortality with implications for no-take reserves. Rev. Fish Biol. Fish. 15 (1), 129–154.

Beard Jr., T.D., Cox, S.P., Carpenter, S.R., 2003. Impacts of daily bag limit reductions on angler effort in Wisconsin walleye lakes. N. Am. J. Fish. Manage. 23, 1283–1293.

Boxrucker, J., 2002. Rescinding a 254-mm minimum length limit on white crappies at Ft. Supply Reservoir, Oklahoma: the influence of variable recruitment, compensatory mortality, and angler dissatisfaction. N. Am. J. Fish. Manage. 22 (4), 1340–1348.

Bryan, H., 1977. Leisure value systems and recreational specialization: the case of trout fishermen. J. Leis. Res. 9 (3), 174–187.

Carpenter, S.R., Brock, W.A., 2004. Spatial complexity, resilience, and policy diversity: fishing on lake-rich landscapes. Ecol. Soc. 9 (1), 8 [online]. Available from www.ecologyandsociety.org/vol9/iss1/art8/.

Chipman, B.D., Helfrich, L.A., 1988. Recreational specializations and motivations of Virginia river anglers. N. Am. J. Fish. Manage. 8 (4), 390–398.

Coggins Jr., L.G., Catalano, M.J., Allen, M.S., Pine III, W.E., Walters, C.J., 2007. Effects of cryptic mortality and the hidden costs of using length limits in fishery management. Fish Fish. 8 (3), 196–210.

Cook, M.F., Goeman, T.J., Radomski, P.J., Younk, J.A., Jacobson, P.C., 2001. Creel limits in Minnesota: a proposal for change. Fisheries 26 (5), 19–26.

Cornelius, R.R., Margenau, T.L., 1999. Effects of length limits on muskellunge in Bone Lake, Wisconsin. N. Am. J. Fish. Manage. 19 (1), 300–308.

Cox, S., Walters, C., 2002. Maintaining quality in recreational fisheries: how success breeds failure in management of open-access sport fisheries. In: Pitcher, T.J., Hollingworth, C.E. (Eds.), Recreational Fisheries: Ecological, Economic and Social Evaluation. Blackwell Publishing, Oxford, U.K., pp. 107–119.

Cox, S.P., Beard, T.D., Walters, C., 2002. Harvest control in open-access sport fisheries: hot rod or asleep at the reel? Bull. Mar. Sci. 70 (2), 749–761.

Cox, S.P., Walters, C.J., Post, J.R., 2003. A model-based evaluation of active management of recreational fishing effort. N. Am. J. Fish. Manage. 23, 1294–1302.

Crawley, M.J., 2007. The R Book. John Wiley & Sons Ltd, Chichester, UK.

Dorow, M., Beardmore, B., Haider, W., Arlinghaus, R., 2010. Winners and losers of conservation policies for European eel, *Anguilla anguilla*: an economic welfare analysis for differently specialised eel anglers. Fish. Manage. Ecol. 17 (2), 106–125.

Dorr, B., Munn, I.A., Meals, K.O., 2002. A socioeconomic and biological evaluation of current and hypothetical crappie regulations in Sardis Lake, Mississippi: an integrated approach. N. Am. J. Fish. Manage. 22 (4), 1376–1384.

Fayram, A.H., Schmalz, P.J., 2006. Evaluation of a modified bag limit for walleyes in Wisconsin: effects of decreased angler effort and lake selection. N. Am. J. Fish. Manage. 26 (3), 606–611.

Fayram, A.H., Hansen, M.J., Ehlinger, T.J., 2006. Influence of walleye stocking on angler effort in Wisconsin. Hum. Dim. Wildl. 11, 129–141.

Fisher, M.R., 1997. Segmentation of the angler population by catch preference, participation, and experience: a management-oriented application of recreation specialization. N. Am. J. Fish. Manage. 17 (1), 1–10.

Fisheries and Oceans Canada, 1990. 1990 Survey of Recreational Fishing in Canada., http://www.dfo-mpo.gc.ca/stats/rec/can/1990/index-eng.htm.

Fisheries and Oceans Canada, 1995. 1995 Survey of Recreational Fishing in Canada., http://www.dfo-mpo.gc.ca/stats/rec/can/1995/index-eng.htm.

Fisheries and Oceans Canada, 2000. 2000 Survey of Recreational Fishing in Canada., http://www.dfo-mpo.gc.ca/stats/rec/can/2000/index-eng.htm.

Gigliotti, L.M., Peyton, R.B., 1993. Values and behaviors of trout anglers, and their attitudes toward fishery management, relative to membership in fishing organizations: a Michigan case study. N. Am. J. Fish. Manage. 13 (3), 492–501.

Hahn, J., 1991. Angler specialization: measurement of a key sociological concept and implications for fisheries management decisions. Am. Fish. Soc. Symp. 12, 380–389.

Hansen, M.J., Beard Jr., T.D., Hewett, S.W., 2000. Catch rates and catchability of walleyes in angling and spearing fisheries in northern Wisconsin lakes. N. Am. J. Fish. Manage. 20 (1), 109–118.

High, B., Meyer, K.A., Schill, D.J., Mamer, E.R.J., 2008. Distribution, abundance, and population trends of bull trout in Idaho. N. Am. J. Fish. Manage. 28 (6), 1687–1701.

Holm, S., 1979. A simple sequentially rejective multiple test procedure. Scand. J. Stat. 6 (2), 65–70.

Hoyle, S.D., Cameron, D.S., 2003. Confidence intervals on catch estimates from a recreational fishing survey: a comparison of bootstrap methods. Fish. Manage. Ecol. 10 (2), 97–108.
Hunt, L., 2005. Recreational fishing site choice models: insights and future opportunities. Hum. Dim. Wildl. 10 (3), 153–172.
Hunt, L., Arlinghaus, R., Lester, N., Kushneriuk, R. The effects of regional angling effort, angler behavior, and harvesting efficiency on landscape patterns of overfishing. Ecol. Appl., in press. doi:10.1890/10-1237.1.
Hurley, K.L., Jackson, J.J., 2002. Evaluation of a 254-mm minimum length limit for crappies in two southeast Nebraska reservoirs. N. Am. J. Fish. Manage. 22 (4), 1369–1375.
Hutt, C.P., Bettoli, P.W., 2007. Preferences, specialization, and management attitudes of trout anglers fishing in Tennessee tailwaters. N. Am. J. Fish. Manage. 27 (4), 1257–1267.
Jacobson, P.C., 1996. Trophy and consumptive value-per-recruit analysis for a walleye fishery. N. Am. J. Fish. Manage. 16 (1), 75–80.
Johnson, B.M., Carpenter, S.R., 1994. Functional and numerical responses: a framework for fish–angler interactions? Ecol. Appl. 4 (4), 808–821.
Johnston, F.D., Post, J.R., 2009. Density-dependent life-history compensation of an iteroparous salmonid. Ecol. Appl. 19 (2), 449–467.
Johnston, F.D., Post, J.R., Mushens, C.J., Stelfox, J.D., Paul, A.J., Lajeunesse, B., 2007. The demography of recovery of an overexploited bull trout, *Salvelinus confluentus*, population. Can. J. Fish. Aquat. Sci. 64 (1), 113–126.
Johnston, F.D., Arlinghaus, R., Dieckmann, U., 2010. Diversity and complexity of angler behaviour drive socially optimal input and output regulations in a bioeconomic recreational-fisheries model. Can. J. Fish. Aquat. Sci. 67 (9), 1507–1531.
Jones, C.M., Robson, D.S., Lakkis, H.D., Kressel, J., 1995. Properties of catch rates used in analysis of angler surveys. Trans. Am. Fish. Soc. 124 (6), 911–928.
Lester, N.P., Marshall, T.R., Armstrong, K., Dunlop, W.I., Ritchie, B., 2003. A broad scale approach to management of Ontario's recreational fisheries. N. Am. J. Fish. Manage. 23, 1312–1328.
Lewin, W.C., Arlinghaus, R., Mehner, T., 2006. Documented and potential biological impacts of recreational fishing: insights for management and conservation. Rev. Fish. Sci. 14, 305–367.
Malvestuto, S.P., 1996. Sampling the recreational creel. In: Murphy, B.R., Willis, D.W. (Eds.), Fisheries Techniques, second ed. American Fisheries Society, Bethesda, MD, pp. 591–623.
Manly, B.F.J., 1997. Randomization, Bootstrap and Monte Carlo Methods in Biology. Chapman & Hall, London, UK.
Metcalf, S.J., Moyle, K., Gaughan, D.J., 2010. Qualitative analysis of recreational fisher response and the ecosystem impacts of management strategies in a data-limited situation. Fish. Res. 106 (3), 289–297.
Mosindy, T., Duffy, M., 2007. The use of angler diary surveys to evaluate long-term changes in muskellunge populations on Lake of the Woods, Ontario. Environ. Biol. Fishes 79 (1), 71–83.
Muoneke, M.I., 1994. Dynamics of a heavily exploited Texas white bass population. N. Am. J. Fish. Manage. 14 (2), 415–422.
Myers, R., Taylor, J., Allen, M., Bonvechio, T.F., 2008. Temporal trends in voluntary release of largemouth bass. N. Am. J. Fish. Manage. 28 (2), 428–433.
Newman, S.P., Hoff, M.H., 2000. Evaluation of a 16-Inch minimum length limit for smallmouth bass in Pallette Lake, Wisconsin. N. Am. J. Fish. Manage. 20 (1), 90–99.
Novinger, G.D., 1987. Evaluation of a 15.0-inch minimum length limit on largemouth bass and spotted bass catches at Table Rock Lake, Missouri. N. Am. J. Fish. Manage. 7 (2), 260–272.
Oh, C.-O., Ditton, R.B., Gentner, B., Riechers, R., 2005. A stated preference choice approach to understanding angler preferences for management options. Hum. Dim. Wildl. 10 (3), 173–186.
Pacas, C., Hunt, B., 2004. Results of Creel Surveys on Lake Minnewanka with Emphasis on 2000. Banff National Park, Parks Canada, 67 pp.
Parker, B.R., Schindler, D.W., Wilhelm, F.M., Donald, D.B., 2007. Bull trout population responses to reductions in angler effort and retention limits. N. Am. J. Fish. Manage. 27 (3), 848–859.
Parkinson, E.A., Post, J.R., Cox, S.P., 2004. Linking the dynamics of harvest effort to recruitment dynamics in a multistock, spatially structured fishery. Can. J. Fish. Aquat. Sci. 61 (9), 1658–1670.
Peterson, J.T., Evans, J.W., 2003. Quantitative decision analysis for sport fisheries management. Fisheries 28 (1), 10–21.
Pollock, K.H., Jones, C.M., Brown, T.L., 1994. Angler Survey Methods and their Applications in Fisheries Management. American Fisheries Society Special Publication 25. American Fisheries Society, Bethesda, MD.
Pollock, K.H., Hoenig, J.M., Jones, C.M., Robson, D.S., Greene, C.J., 1997. Catch rate estimation for roving and access point surveys. N. Am. J. Fish. Manage. 17 (1), 11–19.
Post, J.R., Sullivan, M., Cox, S., Lester, N.P., Walters, C.J., Parkinson, E.A., Paul, A.J., Jackson, L., Shuter, B.J., 2002. Canada's recreational fisheries: the invisible collapse? Fisheries 27 (1), 6–17.
Post, J.R., Mushens, C., Paul, A., Sullivan, M., 2003. Assessment of alternative harvest regulations for sustaining recreational fisheries: model development and application to bull trout. N. Am. J. Fish. Manage. 23 (1), 22–34.
Post, J.R., Persson, L., Parkinson, E.A., van Kooten, T., 2008. Angler numerical response across landscapes and the collapse of freshwater fisheries. Ecol. Appl. 18 (4), 1038–1049.
Quinn, S.P., 1992. Angler perspectives on walleye management. N. Am. J. Fish. Manage. 12 (2), 367–378.
R Development Core Team, 2010. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.R.
Radomski, P.J., Goeman, T.J., 1996. Decision making and modeling in freshwater sport-fisheries management. Fisheries 21 (12), 14–21.
Radomski, P.J., Grant, G.C., Jacobson, P.C., Cook, M.F., 2001. Visions for recreational fishing regulations. Fisheries 26, 7–18.
Rodtka, M., 2009. Status of the bull trout (*Salvelinus confluentus*) in Alberta: Update 2009. Pages 48 in Alberta Wildlife Status Report No. 39 (Update 2009). Alberta Sustainable Resource Development and The Alberta Conservation Association, Edmonton, AB.
Shetter, D.S., Alexander, G.R., 1962. Effects of a flies-only restriction on angling and on fall trout populations in Hunt Creek, Montmorency County, Michigan. Trans. Am. Fish. Soc. 91 (3), 295–302.
Simonson, T.D., Hewett, S.W., 1999. Trends in Wisconsin's muskellunge fishery. N. Am. J. Fish. Manage. 19 (1), 291–299.
Slipke, J.W., Maceina, M.J., Travnichek, V.H., Weathers, K.C., 1998. Effects of a 356-mm minimum length limit on the population characteristics and sport fishery of smallmouth bass in the Shoals Reach of the Tennessee River, Alabama. N. Am. J. Fish. Manage. 18 (1), 76–84.
Stelfox, J.D., 1995. Winter Creel Survey of Lower Kananaskis Lake, December 1991 to March 1992. Unpublished report, Fisheries Management Division, Alberta Environmental Protection. 16 pp.
Stelfox, J.D., 1997. Seasonal movements, growth, survival and population status of the adfluvial bull trout population in Lower Kananaskis Lake, Alberta. In: Mackay, W.C., Brewin, M.K., Monita, M. (Eds.), Friends of the Bull Trout Conference Proceedings. Bull Trout Task Force (Alberta), c/o Trout Unlimited Canada, pp. 309–316.
Sullivan, M.G., 2003. Active management of walleye fisheries in Alberta: dilemmas of managing recovering fisheries. N. Am. J. Fish. Manage. 23 (4), 1343–1358.

Paper II

II

Johnston, F. D., R. Arlinghaus, and U. Dieckmann. 2010. Diversity and complexity of angler behaviour drive socially optimal input and output regulations in a bioeconomic recreational-fisheries model. Canadian Journal of Fisheries and Aquatic Sciences 67(9): 1507-1531.

Johnston, F. D., R. Arlinghaus, and U. Dieckmann. 2010. Erratum: Diversity and complexity of angler behaviour drive socially optimal input and output regulations in a bioeconomic recreational-fisheries model. Canadian Journal of Fisheries and Aquatic Sciences 67(11), 1897-1898.

Diversity and complexity of angler behaviour drive socially optimal input and output regulations in a bioeconomic recreational-fisheries model

Fiona D. Johnston, Robert Arlinghaus, and Ulf Dieckmann

Abstract: In many areas of the world, recreational fisheries are not managed sustainably. This might be related to the omission or oversimplification of angler behaviour and angler heterogeneity in fisheries-management models. We present an integrated bioeconomic modelling approach to examine how differing assumptions about angler behaviour, angler preferences, and composition of the angler population altered predictions about optimal recreational-fisheries management, where optimal regulations were determined by maximizing aggregated angler utility. We report four main results derived for a prototypical northern pike (*Esox lucius*) fishery. First, accounting for dynamic angler behaviour changed predictions about optimal angling regulations. Second, optimal input and output regulations varied substantially among different angler types. Third, the composition of the angler population in terms of angler types was important for determining optimal regulations. Fourth, the welfare measure used to quantify aggregated utility altered the predicted optimal regulations, highlighting the importance of choosing welfare measures that closely reflect management objectives. A further key finding was that socially optimal angling regulations resulted in biological sustainability of the fish population. Managers can use the novel integrated modelling framework introduced here to account, quantitatively and transparently, for the diversity and complexity of angler behaviour when determining regulations that maximize social welfare and ensure biological sustainability.

Résumé : Dans plusieurs régions du monde, les pêches sportives ne sont pas gérées de manière durable. Cela peut être dû à l'omission ou à la sursimplification du comportement et de l'hétérogénéité des pêcheurs dans les modèles de gestion de la pêche. Nous présentons une méthodologie de modélisation bioéconomique intégrée pour examiner comment diverses présuppositions concernant le comportement des pêcheurs, les préférences des pêcheurs et la composition de la population de pêcheurs altèrent les prédictions concernant la gestion optimale des pêches sportives, lorsque les règlementations optimales sont déterminées en maximisant l'utilité globale pour les pêcheurs. Nous présentons quatre résultats principaux issus d'une pêche prototypique au grand brochet (*Esox lucius*). Premièrement, tenir compte du comportement dynamique des pêcheurs modifie les prédictions sur les réglementations optimales de la pêche. Deuxièmement, les régulations optimales des apports et des sorties varient considérablement en fonction des divers types de pêcheurs. Troisièmement, la composition de la population de pêcheurs en ce qui a trait au types de pêcheurs est importante pour déterminer les règlementations optimales. Quatrièmement, la mesure de bien public utilisée pour déterminer l'utilité globale change les réglementations optimales prédites, ce qui souligne l'importance de choisir des mesures de bien public qui reflètent bien les objectifs de gestion. Une autre découverte importante est que des règlementations de pêche optimales du point de vue social résultent en des populations de poissons durables du point vue biologique. Les gestionnaires peuvent utiliser le cadre inédit de modélisation intégré que nous présentons ici pour tenir compte de façon quantitative et transparente de la diversité et de la complexité des comportements des pêcheurs lorsqu'ils mettent en place des règlementations qui maximisent le bien public et assurent la durabilité biologique.

[Traduit par la Rédaction]

Received 27 September 2009. Accepted 20 April 2010. Published on the NRC Research Press Web site at cjfas.nrc.ca on 3 September 2010.
J21433

F.D. Johnston.[1] Evolution and Ecology Program, International Institute for Applied Systems Analysis, Schlossplatz 1, A-2361 Laxenburg, Austria; Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany; Inland Fisheries Management Laboratory, Department for Crop and Animal Sciences, Faculty of Agriculture and Horticulture, Humboldt-University of Berlin, Philippstrasse 13, Haus 7, 10115 Berlin, Germany.
R. Arlinghaus. Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany; Inland Fisheries Management Laboratory, Department for Crop and Animal Sciences, Faculty of Agriculture and Horticulture, Humboldt-University of Berlin, Philippstrasse 13, Haus 7, 10115 Berlin, Germany.
U. Dieckmann. Evolution and Ecology Program, International Institute for Applied Systems Analysis, Schlossplatz 1, A-2361 Laxenburg, Austria.

[1]Corresponding author (e-mail: johnston@iiasa.ac.at).

Introduction

Recreational anglers are the dominant users of most freshwater and some coastal fish stocks in industrialized countries (Arlinghaus and Cooke 2009). Accordingly, managers are faced with the challenge of balancing the interests of angling groups utilizing fisheries resources with concerns about the biological sustainability of exploited fish populations (Radomski et al. 2001; Peterson and Evans 2003; Arlinghaus 2006*b*). The lack of sustainable recreational-fisheries management in some areas of the world (Post et al. 2002; Lewin et al. 2006) suggests that current management strategies have not always been successful in achieving this balance. This may be because effectively managing a fishery requires understanding not only how fish respond to exploitation but also how anglers alter their fishing behaviour in response to social and ecological changes in the fishery; consequently, such behavioural dynamics must be incorporated into integrated fisheries-management models (Johnson and Carpenter 1994; Radomski et al. 2001; Post et al. 2008). In the past, however, recreational-fisheries researchers and managers have focused on the biological dimension of recreational fisheries, largely overlooking the "human dimension" (Aas and Ditton 1998; Cox and Walters 2002*a*; Arlinghaus et al. 2008*a*). To move forward, it is critical to quantify and integrate angler preferences and resulting behavioural decisions into recreational-fisheries models designed to determine optimal management policies (Radomski and Goeman 1996; Arlinghaus et al. 2008*a*).

Optimum social yield (OSY) is one management objective that can incorporate social and economic aspects into fisheries-management models and policies (Roedel 1975). In comparison with the traditional approach of managing for maximum sustainable yield (MSY) in both commercial and recreational fisheries (Larkin 1977; Malvestuto and Hudgins 1996; Hilborn 2007), OSY is better suited to recreational fisheries because it incorporates the sociocultural benefits a fishery provides that are not measured by yield alone, such as an angler's satisfaction resulting from catching a large fish (Roedel 1975; Malvestuto and Hudgins 1996; Radomski et al. 2001). OSY integrates such social and economic factors with biological considerations to develop a fisheries-management objective that maximizes the total utility (alternatively termed benefits or social welfare; Dorow et al. 2010) that a recreational fishery provides to society (Roedel 1975; Malvestuto and Hudgins 1996). Hence, similar to MSY, management for OSY may provide an unambiguous management objective against which to judge management developments and successes (Bennett et al. 1978; Barber and Taylor 1990; Radomski et al. 2001).

Despite the general advantages of a socioeconomic objective such as OSY over MSY for managing recreational fisheries, few recreational-fishing models based on utility theory have been developed to predict the optimal social welfare generated by different management schemes (e.g., Die et al. 1988; Jacobson 1996; Massey et al. 2006). Furthermore, angler-effort dynamics, if considered at all, have generally been assumed to be predominantly or exclusively driven by catch rates or by some other measure of fish abundance (Johnson and Carpenter 1994; Beard et al. 2003; Post et al. 2003). However, angler behaviour is likely much more complex (Carpenter and Brock 2004; Arlinghaus et al. 2008*a*). It is known from social science research on recreational fisheries that, in addition to catch rates, a diverse set of social and biological attributes of a fishery, such as availability of preferred species, fish size, congestion, facilities, regulations, and the perceived aesthetic value of the fishery, affect the participation decisions of anglers (reviewed in Hunt 2005). Therefore, angler-effort dynamics driven by catch rates alone can be unrealistic (Paulrud and Laitila 2004). Hence, recreational-fisheries models designed to maximize angler utility should account for complexity in angler behaviour by incorporating multi-attribute utility functions that describe the fishing participation decisions of anglers.

Another important, yet often overlooked, aspect of recreational fisheries is angler diversity (i.e., heterogeneity in angler behaviour: Anderson 1993; Jacobson 1996; Post et al. 2008). Various types of anglers will differ not only in their fishing preferences, and therefore in the utility they derive from fishing (Fisher 1997; Connelly et al. 2001; Arlinghaus et al. 2008*b*), but also with respect to their fishing practices (Bryan 1977; McConnell and Sutinen 1979; Hahn 1991). Hence, the potential impacts of fishing on fish populations likely vary with angler type (Dorow et al. 2010). For example, in many fisheries, a minority of anglers catches the majority of fish (Baccante 1995), and this minority typically encompasses the most avid and specialized angler types (Dorow et al. 2010). Human dimensions researchers have repeatedly highlighted that accounting for angler diversity is important for sustainable fisheries management (Fisher 1997; Aas et al. 2000; Arlinghaus and Mehner 2003). While there are some examples of coupled social–ecological models that link complex angler behaviour and fish population dynamics (e.g., Cole and Ward 1994; Woodward and Griffin 2003; Massey et al. 2006), to our knowledge, only McConnell and Sutinen (1979) and Anderson (1993) considered heterogeneity in either angler preferences or angler fishing practices in a bioeconomic modelling context. In both cases, the modelling frameworks differed substantially from that presented here. In particular, these earlier studies did not use random-utility models to predict angler participation under different management scenarios, and the complexity of the biological and angler-behaviour components was much more simplified.

The goals of this study were fourfold. First, we present an integrative bioeconomic modelling approach that links the ecological, socioeconomic, and management components driving angler-effort dynamics to a fish population model. With this model, optimal harvest regulations for various angler types were predicted. Second, we demonstrate the importance of assumptions about angler-effort dynamics in fisheries management by contrasting predictions from models that make traditional assumptions of static or exclusively catch-based dynamic angler behaviour with models that assume more complex, multi-attribute dynamic behaviour. In this study, complexity in angler behaviour is characterized by whether angler-effort dynamics rely on a single fishery attribute to drive angler behaviour or on multiple fishery attributes. Third, by incorporating heterogeneity in angler behaviour into a bioeconomic modelling framework by accounting for the perceived utility a fishery provides to an angler population, we examined how angler diversity (i.e.,

heterogeneity of angler types) and the composition of the angler population (in terms of these angler types) influenced predictions about optimal management strategies. Finally, we explored how different management objectives, represented by different measures of social welfare, altered predicted optimal management regulations. Rather than simulating a particular fishery, our approach is stylized in nature and is intended to demonstrate the suitability of an integrated bioeconomic modelling approach for investigating coupled angler–fish population dynamics.

Materials and methods

We developed an integrated model in which angler-type-specific utility derived from both catch- and non-catch-related attributes of the fishing experience was linked to a deterministic age-structured fish population model for a single-species, single-lake fishery. Our modelling framework had three components: (*i*) a management component that described the regulations applied to the fishery system, (*ii*) a socioeconomic component that described the effort dynamics of different angler types, and (*iii*) a biological component that described the fish population dynamics. Angler utility was used to determine changes in angling effort in the dynamic angler-behaviour scenarios and to make predictions about optimal harvest regulations. The resulting impacts on the fish population under different management policies were investigated to determine whether management for social optima also conserved the fish population (all model equations are summarized in Table 1 and illustrated in Fig. 1; model parameters are listed in Tables 2 and 3).

Management component

Traditional harvest-control measures have focused on regulating the harvest rates of individual anglers to achieve biological sustainability (Radomski et al. 2001). However, in open-access systems, which are typical for many recreational fisheries (Post et al. 2002), output regulations that do not directly limit angler numbers cannot constrain total fishing mortality (Radomski et al. 2001; Cox and Walters 2002*a*, 2002*b*). The failure of traditional output regulations to preserve some recreationally exploited fish populations (Post et al. 2002) has led to a call for input regulations that more directly limit angling effort (Cox and Walters 2002*a*, 2002*b*). Therefore, we investigated two types of regulatory policies over a range of values (Table 2): a traditional output regulation, expressed in terms of a minimum-size limit, and an input regulation, expressed in terms of the number of angling licenses issued.

Socioeconomic component

Angler utility

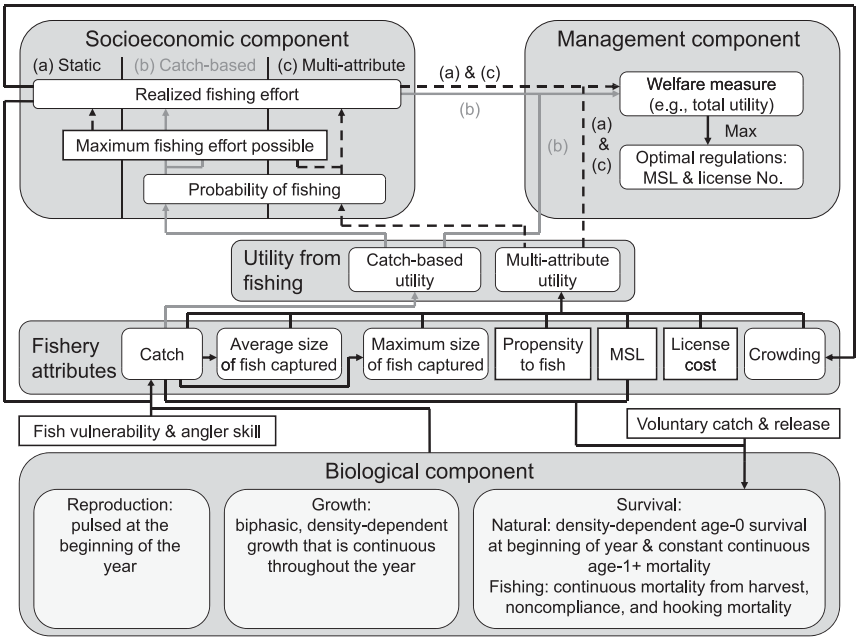
Economic utility theory assumes that human agents make choices that will maximize their personal utility (alternatively termed benefits or satisfaction; Perman et al. 2003). For example, from a set of potential alternatives, recreational anglers will choose to fish a fishery that provides them with the greatest possible utility (Hunt 2005). Multiple attributes contribute to an individual angler's utility function, and the relative importance of fishery attributes (such as fish size or crowding), called part-worth-utilities, for total angler utility varies substantially among different angler types (Aas et al. 2000; Oh et al. 2005*a*; Oh and Ditton 2006). Choice models based on random-utility theory (McFadden 1974; Manski 1977) can be calibrated with actual (revealed) or hypothetical (stated) empirical site-choice data. Such models constitute one approach that can be used to predict recreational angler behaviour, which can then be used to predict and understand how anglers will react to changes in the attributes of a fishery (Paulrud and Laitila 2004; Massey et al. 2006; Wallmo and Gentner 2008).

Three scenarios of angler behaviour were investigated. In the first scenario, we simulated static angler behaviour, characterized by anglers that did not respond to changes in a fishery's attributes (such as fish size, catch rate, or congestion level) but instead participated at the maximum effort level allowed. Predictive recreational-fisheries models often assume constant exploitation rates and ignore angler dynamics when evaluating regulation impacts (e.g., Dunning et al. 1982). The static scenario mimics this situation by keeping angling effort constant. In our two other scenarios, anglers were allowed to behave dynamically, i.e., they chose to fish or not to fish depending on the time-varying utility provided by the fishery. Utility functions that described the preferences of a particular angler type for the fishing attributes experienced were used to simulate angler-type-specific behavioural decisions. In the second scenario, the utility of fishing was based on the utility gained from catch rates alone (Table 1, eq. 1*a*; Table 3), an approach used in previous recreational-fishing models (Cox et al. 2003; Post et al. 2003). In the third scenario, utility was based on a more realistic multi-attribute utility function (Table 1, eq. 1*b*; Table 3). Attributes included in this utility function were catch rates, average size of fish caught, maximum size of fish caught, angler congestion, minimum-size limit regulations, and license costs, all of which have been shown to affect anglers' decisions about participating in a particular fishery (Hunt 2005). Although the multi-attribute utility function was not used to determine angling effort in the static scenario, for comparative purposes, it was used to evaluate the quality of the fishery at the end of the simulations (Table 1, eq. 1*b*; Fig. 1).

Angler-effort dynamics

In our second and third scenarios, anglers responded dynamically to their perception of fishery quality by changing the amount of effort they devoted to the fishery. In these scenarios, the utility gained from a fishing experience determined the angler's probability of choosing to fish over the alternative of not fishing (Table 1, eq. 2*a*). This probability was calculated as is typical in empirical choice models (Oh et al. 2005*b*; Massey et al. 2006). The probability of fishing based on angler utility as well as the maximum time anglers would fish in a year irrespective of fishing quality were then used to determine the realized annual effort of anglers (i.e., the amount of time they actually fished: Table 1, eqs. 2*b*–2*e*; Fig. 1). To account for the fact that anglers make decisions based on previous experiences and habits and not exclusively based on their most recent experiences (Adamowicz et al. 1994), a fishing-behaviour persistence term (Table 2) was introduced into the effort dynamics (Table 1, eq. 2*b*). This term described the relative influence of last year's real-

Fig. 1. Simplified flow diagram illustrating interactions among the three model components of our bioeconomic modelling approach: the biological component, the socioeconomic component, and the management component. The model included three angler-behaviour scenarios: (*a*) static angler behaviour, where anglers fished at the maximal rate, (*b*) catch-based dynamic angler behaviour, where anglers responded to the fishery based on catch rates, and (*c*) multi-attribute dynamic angler behaviour, where anglers responded to the fishery based on a multi-attribute utility function. Black solid arrows depict influences that apply across all scenarios, while gray arrows apply to the catch-based scenario only and black broken arrows apply to either the static or multi-attribute scenario, as is also indicated by labels beside the arrows. Factors in round-cornered boxes dynamically changed throughout model runs, while parameters for factors in square-cornered boxes were held constant.



ized fishing probability on the current year's realized fishing probability. We assumed that the realized annual angling effort (Table 1, eq. 2*e*) was limited by three factors: the realized probability of fishing, the desired maximum effort according to which an individual angler would fish irrespective of angling quality (Table 1, eq. 2*c*), and the input regulation expressed in terms of the number of angling licenses issued (Table 1, eq. 2*d*). The instantaneous fishing effort of a given angler type was assumed to be constant throughout the fishing season and to equal zero after the fishing season ended (Table 1, eq. 2*f*).

Angler heterogeneity

Angler heterogeneity was introduced into our model by defining three different angler types, generic, consumptive, and trophy anglers, that differed in their degree of angling specialization (Bryan 1977; Ditton et al. 1992) (Table 3). Our parameterization of angler behaviour was based on recreational specialization theory (Bryan 1977; Ditton et al. 1992). Bryan (1977) described four general angler types ranging from the casually involved to the technique and setting specialist. As specialization levels increase, skill levels improve, fish size is of greater importance, and harvesting fish is of lesser importance (Bryan 1977). This can lead to differing propensities to perform voluntary catch-and-release (Arlinghaus 2007) and to an increased ability to catch more and larger fish (Dorow et al. 2010). Angler preferences also change with specialization: for example, the value of solitude relative to the social aspects of the fishing experience varies with specialization (Ditton et al. 1992; Connelly et al. 2001). Based on pioneering work by Bryan (1977) and subsequent applications and refinements (e.g., Quinn 1992; Allen and Miranda 1996; Fisher 1997), we devised qualitatively realistic angler-type-specific part-worth-utility functions for the various attributes of the fishing experience. Qualitative differences in preferences and tolerances for different fishery attributes among angler types are illustrated in Fig. 2 and the resultant utility functions in Fig. 3.

Parameters for three stylized angler types were chosen to reflect differential skill, consumptive orientation, and overall dedication to the recreational-fishing experience (Table 3). Angler types differed in both their fishing practices and their preferences for various attributes of the fishing experience (Fig. 2; Table 3). Generic anglers were assumed to be the least specialized, consumptive anglers were intermediate, and trophy anglers were the most specialized. By definition, consumptive anglers had the greatest consumptive orientation. Accordingly, generic anglers were assumed to (*i*) be least likely to participate in angling activities, (*ii*) be intermediate in their tolerance of restrictive minimum-size limits, (*iii*) be the most affected by license costs, (*iv*) have an intermediate interest in catch rates and be least interested in the challenge of catching fish, (*v*) be least interested in average fish size and be intermediately interested in trophy-sized

Fig. 2. Qualitative differences in angler preferences for fishery attributes among the three different prototypical angler types (generic, consumptive, and trophy anglers). Gray circles indicate the relative preference levels or tolerance levels (low, intermediate, or high) of angler types for a particular fishery attribute.

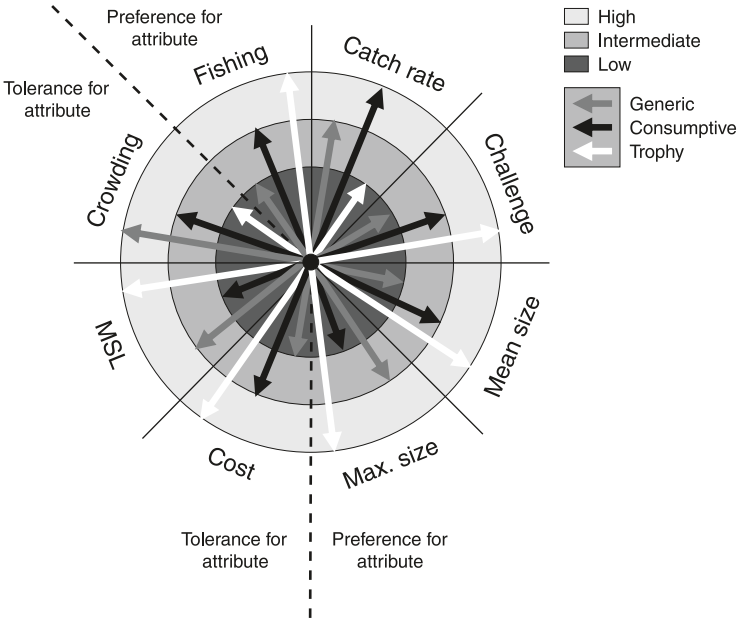
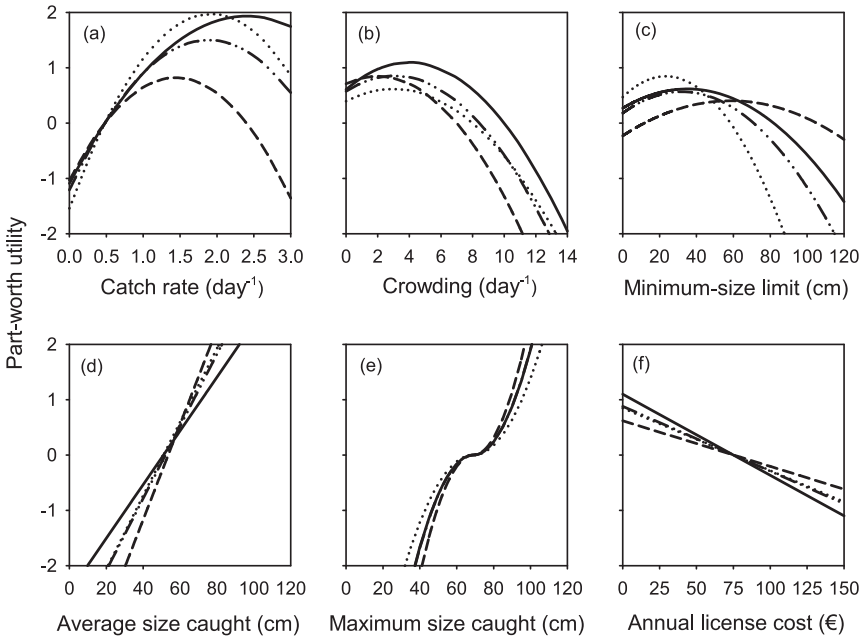


Fig. 3. Part-worth-utility functions describing the preferences of generic (solid line), consumptive (dotted line), trophy (dashed line), and average (dash-dotted) anglers for various attributes of the fishery.



fish, (*vi*) be most tolerant of angler crowding, (*vii*) be least skilled, and (*viii*) practice some voluntary catch-and-release of harvestable fish (Table 3). In contrast, consumptive anglers were assumed to (*i*) participate at an intermediate level in angling activities, (*ii*) be least tolerant of restrictive minimum-size limits, (*iii*) be intermediately affected by license costs, (*iv*) be most interested in catch rates and intermediately interested in the challenge of catching fish, (*v*) be intermediately interested in average fish size and least interested in trophy-sized fish, (*vi*) be intermediately tolerant

of angler crowding, (*vii*) have intermediate skills, and (*viii*) practice no voluntary catch-and-release of harvestable fish (Table 3). Finally, trophy anglers were assumed to (*i*) participate the most in angling activities, (*ii*) be most tolerant of restrictive minimum-size limits, (*iii*) be least affected by license costs, (*iv*) be least interested in catch rates but most interested in the challenge of catching fish, (*v*) be most interested in average fish size and trophy-sized fish, (*vi*) be least tolerant of angler crowding, (*vii*) have the greatest skills, and (*viii*) practice the most voluntary catch-and-release of harvestable fish (Table 3). Trophy anglers were also assumed to target larger fish relative to consumptive and generic anglers (through the use of different fishing gear; Rapp et al. 2008) (Table 3). Parameter values and further justification for these assumptions are provided in Table 3, and the resulting shapes of the angler-type-specific part-worth-utility functions are illustrated in Fig. 3. Although these functions might look different for particular fisheries, we believe that their general features adequately reflect the angling behaviour and preferences of differently specialized recreational anglers.

The importance of angler heterogeneity for determining optimal fishing regulations was examined by first comparing model results among different homogeneous angler populations, each composed of a single angler type. However, because in reality angler populations likely comprise a mixture of angler types, we also considered a mixed angler population composed of all three angler types mentioned above. As this aspect increases the model complexity and in an attempt to simplify angler descriptions, recreational-fisheries researchers and managers may wish to simplify angler descriptions by assuming some form of average angler behaviour (Hahn 1991; Aas and Ditton 1998). Therefore, to examine the importance of explicitly accounting for the composition of the angler population for model predictions of optimal regulations, we compared model results for an average angler-type population with those for a corresponding mixed angler population composed of three angler types. Here, the average angler type was defined by a weighted average of fishing preferences and fishing practices of the three angler types according to their relative frequencies in the mixed angler population (Table 2). Since this is a weighted average, it depends on the assumptions about the relative abundance of angler types in the mixed angler population. This does not, however, affect the capacity of this example to illustrate the implications of the simplifying assumption of an average angler type.

Biological component

Our study aimed to show how the biological and socioeconomic and management components of recreational-fishery systems could be linked in an integrated modelling framework. For brevity, we therefore only describe the essentials of the biological component in terms of growth, reproduction, and survival functions (Tables 1 and 2 provide further details about equations and parameters).

In short, an age-structured model was used to describe the fish population being exploited. Individual fish within an age class were assumed to be ecologically equivalent (Table 1, eqs. 3*a* and 3*b*). The fish population model was parameterized to be representative of a northern pike (*Esox lucius*) population. We chose this species due to its importance to recreational fisheries in both North America and Eurasia (Paukert et al. 2001; Arlinghaus and Mehner 2004*a*). In all scenarios, the fish population reached its demographic equilibrium prior to the introduction of fishing, and the results presented correspond to equilibrium conditions after fishing was introduced (i.e., we investigated long-term dynamics).

The determination of fishing effort (Table 1, eqs. 2*a*–2*f*) and fish reproduction (Table 1, eqs. 5*a*–5*d*) was assumed to occur on an annual basis at the beginning of each year, and population and fishery characteristics were updated annually. However, because recreational fishing is often a size-selective process (Lewin et al. 2006) occurring throughout the year, we described fish mortality and the growth in body size of fish by continuous functions (Table 1, eqs. 4*a*–4*e*). This allowed our model to account for fish to grow into vulnerable size classes within each year and for the recapture and repeated exposure to hooking mortality of released individuals throughout the fishing season, both of which are important aspects of recreational fisheries (Coggins et al. 2007). The resultant ordinary differential equations were solved numerically using the ODE45 function in Matlab (version 7.0.1) (The MathWorks Inc., Natick, Massachusetts).

Two crucial density-dependent relationships were included to allow for compensatory responses of the fish population to exploitation (Lorenzen and Enberg 2002): density-dependent biphasic growth in body size (Table 1, eqs. 4*a*–4*d*) (Lester et al. 2004; Dunlop et al. 2007) and density-dependent survival from spawning to posthatch of fish of age 0. The latter was represented by a Beverton–Holt type relationship, which was assumed to apply at the beginning of each year (Table 1, eq. 5*c*) (Lorenzen 2008). Fish younger than 1 year were assumed to experience no further natural mortality (Table 2) but could experience fishing mortality if they became large enough. Fish 1 year and older experienced a constant natural mortality rate in addition to size-dependent fishing mortality (Table 2, eq. 7*h*).

Fishing mortality was assumed to be size dependent in two ways that quantitatively differed among angler types (see Table 3 for angler-specific parameters). First, catch rates were dependent on the size-dependent vulnerability of fish to the specific fishing gear utilized by each angler type. Vulnerability to capture therefore differed among age classes and also changed over the course of the growing season (Table 1, eqs. 7*a* and 7*b*; see Table 3 for parameters). Catch rates were also dependent on fishing effort and the skill level of the anglers (Table 1, eq. 7*b*; see Table 3 for parameters). Second, harvest of fish was regulated by a minimum-size limit (Table 1, eq. 7*c*). While all fish above the minimum-size limit were harvestable, a portion of undersized fish were also considered harvestable because of noncompliance with regulations (either through ignorance or choice; Sullivan 2002). Anglers chose to harvest fish based on their catch rates mediated by their propensity to voluntarily release fish (Table 1, eq. 7*e*), which was in turn determined by the personal limit an angler had on the number of fish they harvested in a day (see Table 3 for angler-type-specific parameters). Released fish were assumed to experience hooking mortality from handling or injuries (Table 1,

eq. 7*f*; Table 3) (Arlinghaus et al. 2007, 2008*c*). Fish under the minimum-size limit, which were not part of the pool of illegally harvestable fish, only experienced hooking mortality (Table 1, eq. 7*g*).

After fishing was introduced, the fish population was allowed to equilibrate. The spawning-potential ratio was used to assess the biological impacts of angling exploitation. The spawning-potential ratio, which has previously been used in recreational-fishing models (Coggins et al. 2007; Allen et al. 2009), measures reductions in a fish stock's reproductive output and can thus serve as an indicator of recruitment overfishing (Goodyear 1993; Coggins et al. 2007; Allen et al. 2009). Our model used a weighted spawning-potential ratio (Table 1, equations 5*b* and 6). Depending on the life history of a species, values below 0.2–0.3 are considered critically low (Goodyear 1993) and it is commonly assumed that spawning-potential ratio should be maintained above 0.35–0.40 to reduce the risk of recruitment failure (Goodyear 1993; Coggins et al. 2007). We used these values to assess the risk of recruitment overfishing under different management policies.

Social-welfare measures

Social welfare was used to determine optimal regulations. Social welfare is an aggregation of individual utilities (Perman et al. 2003) and determines the total socioeconomic value of a good or service, such as a recreational-fishing experience, as perceived by anglers (Edwards 1991). A social-welfare function describes how individual utilities are aggregated based on their social "worth", and it is assumed that any concerns about equity are accounted for in the aggregation method (Perman et al. 2003). However, maximizing social welfare does not necessarily result in an equitable distribution of resources among individuals, nor is there universal consensus on what constitutes an appropriate social-welfare measure or function (Perman et al. 2003). Managers must therefore carefully decide what social-welfare measures reflect their management objectives (e.g., maximizing angler satisfaction and (or) participation).

In most model simulations described below, a utilitarian social-welfare function was used, referred to as total utility, in which individual utilities were weighted equally among angler types. However, in a subset of simulations, three different social-welfare functions, representing different management objectives, were used to examine how these differences altered predictions about socially optimal management regulations. The first welfare measure, total utility, described the utility gained by an angler type per fishing experience multiplied by the total annual number of fishing experiences (measured in terms of angling effort and expressed in angling days) by that angler type and summed over all angler types (Table 1, eq. 8*a*; similar to McConnell and Sutinen 1979). Total utility reflects the realized demand for angling experiences. However, total utility may be influenced heavily by individuals with disproportionately large utility, and a more equitable distribution of resources among all anglers in the angler population may be desired (Loomis and Ditton 1993). Thus, a second, more equitable utilitarian social-welfare function was examined. Here, individual utility from a fishing experience was weighted by the relative abundance of angler types in the angler population to create a weighted mean utility for an individual, which was then multiplied by the aggregate number of angling days (Table 1, eq. 8*b*). Finally, we examined a Rawlsian approach to utility maximization where the utility of the worst-off individual was maximized, emphasizing the objective of achieving the most equitable distribution of resources (Perman et al. 2003). Here, the utility from the angler type with the lowest individual utility was used and multiplied by the aggregate number of angling days (Table 1, eq. 8*c*). Naturally, the second and third social-welfare measures only differed from the first measure in the mixed angler population composed of different angler types.

Outline of analysis

Across a range of minimum-size limits and angling license numbers, three different angler-behaviour scenarios, static, catch-based dynamic, and multi-attribute dynamic scenarios, were considered for five different types of angler populations: generic, consumptive, trophy, average, and mixed. Optimal input and output regulations were identified by maximizing one of three measures of social welfare: total utility, equitable utilitarian utility, and Rawlsian utility (Table 1, eqs. 8*a*–8*c*). With this approach, we examined the impacts of dynamic angler behaviour, angler heterogeneity, and composition of the angler population on socially optimal regulations and the resulting biological impacts on the fish population. In most analyses presented, total utility was used to determine socially optimal management regulations. However, we also examined the equitable utilitarian utility and Rawlsian-utility social-welfare measures in the context of multi-attribute dynamic angler behaviour and mixed angler populations to demonstrate how different management objectives altered socially optimal management regulations.

We used sensitivity analyses to explore the importance of different attributes for determining angler behaviour, optimal regulations, and biological impacts by removing in turn each attribute from the multi-attribute angler-behaviour scenario. However, given the hypothetical nature of the constructed angler types and their part-worth-utility functions (Fig. 3), we decided it would be imprudent to derive generalized conclusions about the relative importance of individual attributes in determining optimal regulations. Therefore, sensitivity analyses were not intensified beyond the approach summarized above.

Results

Impacts of dynamic angler behaviour

A comparison of the three angler-behaviour scenarios showed substantial differences in predictions of total utility (left to right in Fig. 4). Optimal minimum-size limits were predicted to be highest in scenarios with catch-based dynamic angler behaviour and were generally lower (and similar) for corresponding scenarios with static and multi-attribute dynamic angler behaviour for angler populations composed of one angler type (Table 4; Fig. 4). Optimal effort regulations were lowest in the static scenarios, intermediate in the multi-attribute scenarios, and highest in the catch-based scenarios (Table 4). In fact, optimal license numbers in the catch-based scenarios were often more than two times larger than in the other scenarios. Under predicted

Table 1. Model equations.

Eq.		Description
Individual-angler utility		
[1*a*]	$U_{fj} = U_{cj}$	Conditional indirect utility gained by an angler of type j from choosing to fish (catch-based scenario only)
[1*b*]	$U_{fj} = U_{0j} + U_{cj} + U_{sj} + U_{xj} + U_{aj} + U_{rj} + U_{oj}$	Conditional indirect utility gained by an angler of type j from choosing to fish (static and multi-attribute scenarios)
Angler-effort dynamics		
[2*a*]	$p_{fj} = \exp(\widehat{U}_{fj})/\exp(U_n) + \exp(\widehat{U}_{fj})$	Probability that an angler of type j chooses to fish over the alternative to not fish, where $\widehat{U}_{fj}$ applies to the previous year
[2*b*]	$p_{Fj} = (1-\varphi)p_{fj} + \varphi\widehat{p}_{Fj}$	Realized probability that an angler of type j chooses to fish, where $\widehat{p}_{Fj}$ applies to the previous year
[2*c*]	$D_j = p_{Fj}/D_{max}$	Number of days an angler of type j chooses to fish during a year
[2*d*]	$A_{Lj} = \rho_j A_L$	Number of licensed anglers of type j
[2*e*]	$E_j = D_j A_{Lj} \Psi/\phi$	Total annual realized fishing effort per unit area of all anglers of type j
[2*f*]	$e_{jt} = \begin{cases} E_j/S_F & \text{if } t \le S_F \\ 0 & \text{if } t > S_F \end{cases}$	Instantaneous fishing effort per unit area at time t of all anglers of type j
Age-structured fish population		
[3*a*]	$N_{total} = \sum_{a=0}^{a_{max}} N_a$	Total fish population density
[3*b*]	$B_{total} = \sum_{a=0}^{a_{max}} N_a W_a$	Total fish biomass density
Growth		
[4*a*]	$h = h_{max}/(1 + B_{total}/B_{1/2})$	Maximum annual growth of a fish dependent on the biomass density at the beginning of the year
[4*b*]	$p_a = \begin{cases} 1 - \dfrac{G}{3+G}(1 + L_{a0}/h) & \text{if } a \ge a_m - 1 \\ 1 & \text{if } a < a_m - 1 \end{cases}$	Proportion of the growing season during which a fish of age a allocates energy to growth
[4*c*]	$g_{at} = \begin{cases} h/S_G & \text{if } t \le p_a S_G \\ 0 & \text{if } t > p_a S_G \end{cases}$	Instantaneous growth rate in length of a fish of age a at time t
[4*d*]	$L_{at} = L_{a0} + g_{at}t$	Length of a fish of age a at time t
[4*e*]	$W_{at} = wL_{at}^l$	Mass of a fish of age a at time t
Reproduction		
[5*a*]	$R_a = \begin{cases} \delta W_a \mathrm{GSI}/W_e & \text{if } a \ge a_m \\ 0 & \text{if } a < a_m \end{cases}$	Annual fecundity of a female fish of age a
[5*b*]	$b = \Phi \sum_{a=a_m}^{a_{max}} R_a N_a$	Annual population fecundity density, pulsed at the beginning of the year
[5*c*]	$s_0 = \alpha/(1 + b/b_{1/2})$	Survival probability from spawning to posthatch of fish of age 0, applied at the beginning of the year
[5*d*]	$N_0 = s_0 b$	Density of age 0 fish at the beginning of the year
[6]	$\mathrm{SPR} = b_F/b_U$	Spawning-potential ratio (= relative reduction in egg production under fishing relative to the corresponding unfished condition)

Published by NRC Research Press

Table 1 (*concluded*).

Eq.		Description
Mortality		
[7*a*]	$v_{ajt} = [1 - \exp(-y_j L_{at})]^{z_j}$	Proportion of fish of age a that are vulnerable to capture by anglers of type j at time t
[7*b*]	$c_{ajt} = q_j e_{jt} v_{ajt}$	Instantaneous per capita catch rate of fish of age a by anglers of type j at time t
[7*c*]	$H_{ajt} = \begin{cases} 1 & \text{if } L_{at} \geq \text{MSL} \\ f_{\text{nj}} & \text{if } L_{at} < \text{MSL} \end{cases}$	Proportion of fish at age a that are harvestable by anglers of type j at time t
[7*d*]	$C_{jt} = \sum_{a=0}^{a_{\max}} c_{ajt} N_a H_{ajt}$	Instantaneous catch rate of harvestable fish by anglers of type j at time t
[7*e*]	$C_{\text{H}jt} = \min(C_{jt}, c_{\max j}, e_j/\Psi)$	Instantaneous harvest rate by anglers of type j at time t
[7*f*]	$f_{\text{H}jt} = \frac{C_{\text{W}jt}}{C_{jt}} + f_{\text{h}j} \frac{C_{jt} - C_{\text{W}jt}}{C_{jt}}$	Proportion of vulnerable harvestable fish killed by anglers of type j at time t
[7*g*]	$m_{\text{f}ajt} = f_{\text{H}jt} c_{ajt} H_{ajt} + f_{\text{h}j} c_{ajt} (1 - H_{ajt})$	Instantaneous per capita fishing mortality rate of fish of age a imposed by anglers of type j at time t
[7*h*]	$d_{at} = m_{\text{n}a} + \sum_j m_{\text{f}ajt}$	Instantaneous per capita mortality rate of fish of age a at time t
[7*i*]	$\text{d}N_a/\text{d}t = -d_{at} N_a$	Continuous rate of change in the density of fish of age a at time t
Social-welfare measures		
[8*a*]	$U_{\text{TU}} = \sum_j U_{\text{f}j} D_j A_{\text{L}j}$	Annual total utility
[8*b*]	$U_{\text{EU}} = \sum_j (U_{\text{f}j} \rho_j) \sum_j (D_j A_{\text{L}j})$	Annual equitable utilitarian utility
[8*c*]	$U_{\text{RU}} = \min_j (U_{\text{f}j}) \sum_j (D_j A_{\text{L}j})$	Annual Rawlsian utility

Note: The modelled species was northern pike (*Esox lucius*). Variables, parameters, parameter values, and their sources are listed in Table 2. Angler types are specified in Table 3.

Table 2. Model variables, parameters, parameter values, and their sources.

Symbol	Description (units where applicable)	Equation	Value or range	Source
Index variables				
j	Angler type		Generic, consumptive, trophy, or average	
a	Age class (years)		0–a_{max}	
a_{max}	Maximum age of a fish (years)		15	1
t	Time within the year (years)		0–1	
Angling regulations				
MSL	Minimum-size limit (cm)	7*c*	0–120	
A_L	Number of angling licenses (= number of licensed anglers)	2*d*	0–100	
Angler population				
ρ_j	Proportion of the angler population that is composed of anglers of type j	2*d*, 8*b*	Nonmixed: 1.0 for one j, 0.0 for the others; mixed: 0.4, 0.3, 0.3, 0.0	
Angler-effort dynamics				
U_n	Conditional indirect utility gained by an angler from choosing not to fish	2*a*	0	
φ	Persistence of fishing behaviour (= the relative influence of last year's realized fishing probability on the current year's realized fishing probability)	2*b*	0.5	
Ψ	Average time an angler will fish in a day (h)	2*e*	4	—[a]
D_{max}	Maximum number of days that an angler would fish per year irrespective of fishing quality	2*c*	40	—[a]
ϕ	Lake area (ha)	2*e*	100	
S_F	Annual duration of the fishing season (years)	2*f*	9/12	
Age-structured fish population				
N_a	Density of fish of age a (ha^{-1})	3*a*, 3*b*, 5*b*, 5*d*, 7*d*	0–∞	
Growth				
h_{max}	Maximum growth increment (cm)	4*a*	24.0	—[b]
$B_{1/2}$	Total fish biomass density at which the growth increment is halved (kg·ha^{-1})	4*a*	100.0	—[b]
G	Annual reproductive investment	4*b*	0.58	—[b]
a_m	Age at first spawning (years)	4*b*, 5*a*	2	4
L_{a0}	Length of fish of age a at the beginning of a year (cm)	4*b*	0–∞	
L_0	Length of fish at hatch (cm)	4*b*	0.8	2
S_G	Annual duration of the growing season (years)	4*c*	1.0	
w	Scaling constant for length–mass relationship (g·cm^{-l})	4*e*	0.0048	6
l	Allometric parameter for length–mass relationship	4*e*	3.059	6
Reproduction				
GSI	Gonadosomatic index (= gonadic mass/somatic mass)	5*a*	0.17	3
W_e	Average egg mass (g)	5*a*	0.0050	3
δ	Proportion of eggs that hatch	5*a*	0.75	4
Φ	Proportion of female fish in the spawning population	5*b*	0.5	5
α	Maximum proportion of offspring surviving from spawning to posthatch	5*c*	4.75×10^{-4}	—[c]
$b_{1/2}$	Annual population fecundity density at which survival of offspring from spawning to posthatch is halved (ha^{-1})	5*c*	20 325	—[c]
b_F	Annual population fecundity under fishing	6	0–∞	
b_U	Annual population fecundity under unfished conditions	6	0–∞	
Mortality				
m_{na}	Instantaneous natural mortality rate of fish of age a (year^{-1})	7*h*	0.00 if $a = 0$, 0.42 if $a > 0$	4

Note: Source: 1, Craig and Kipling 1983; 2, Frost and Kipling 1967; 3, Hubenova et al. 2007; 4, Kipling and Frost 1970; 5, Le Cren et al. 1977; 6, Willis 1989. The modelled species was northern pike (*Esox lucius*). Equations are listed in Table 1. Angler types are specified in Table 3.

[a]Estimated from average participation rates and average lengths of fishing trips obtained from diary data of recreational anglers in Mecklenburg-Vorpommern, Germany (M. Dorow and R. Arlinghaus, unpublished data) and other literature (van Poorten and Post 2005; Post et al. 2008).

[b]Estimated from empirical length-at-age and biomass density data from various pike studies (Kipling and Frost 1970; Kipling 1983*a*; Treasurer et al. 1992; Pierce and Tomcko 2003, 2005; Pierce et al. 2003) by minimizing the sum of squares using the "solver" function in Excel (Microsoft Office Excel 2003).

[c]Estimated from modified data on female biomass and age-2 abundance in Lake Windermere (Kipling 1983*b*). Egg density was determined using the relative fecundity relationship reported in Craig and Kipling (1983) and adult biomass from Kipling (1983*b*), and natural mortality information from Kipling and Frost (1970) was used to calculate age-1 abundance from age-2 abundance.

Published by NRC Research Press

Table 3. Angler types and their angling behaviour described by part-worth-utility (PWU) functions.

Variable	Symbol and defining equation (affected equation); rationale for general shape (source)	Rationale for angler-type-specific shape (source)	Parameters values describing angler types			
			Generic	Consumptive	Trophy	Average
Importance of fishing to angler lifestyle						
Basic utility gained by an angler of type j from choosing to fish	U_{0j} (eq. 1*b*); constant function: the propensity to fish when all other attributes are as expected; see footnotes for expected values[b,c,d]	As specialization increases: basic utility of fishing increases (4, 16); the assumed annual participation is generally consistent with study findings (7, 10)	Lowest: U_{0j} = –0.405 (40% probability of fishing)	Intermediate: U_{0j} = 0.000 (50% probability of fishing)	Highest: U_{0j} = 0.405 (60% probability of fishing)	U_{0j} = –0.041 (49% probability of fishing)
Tolerances with regard to managerial constraints						
PWU of minimum-size limit for an angler of type j	$U_{rj} = u_{1j}r + u_{2j}r^2 + u_{3j}$ (eq. 1*b*), where r is the standardized MSL[a];dome-shaped quadratic function: anglers may prefer moderate minimum-size regulations but object to too low and to too high levels (10, 16, 17)	As specialization increases: anglers become less consumptive and have a greater acceptance of stricter minimum-size regulations (6, 16) but consumptively oriented anglers are averse to harvest regulations that limit their ability to harvest fish (1, 8, 12)	Intermediate: u_{1j} = 2.321, u_{2j} = –3.869, u_{3j} = 0.271	Lowest: u_{1j} = 3.766, u_{2j} = –9.414, u_{3j} = 0.471	Highest: u_{1j} = 2.534, u_{2j} = –2.534, u_{3j} = –0.228	u_{1j} = 2.819, u_{2j} = –5.132, u_{3j} = 0.181
PWU of annual license cost for an angler of type j	$U_{oj} = u_{4j}o$ (eq. 1*b*), where o is the relative license cost[b]; linear function: license costs usually have a negative effect on angler utility (14, 21)	As specialization increases: cost aversion decreases (4, 16)	Lowest: u_{4j} = –0.015·€$^{-1}$	Intermediate: u_{4j} = –0.011·€$^{-1}$	Highest: u_{4j} = –0.008·€$^{-1}$	u_{4j} = –0.012·€$^{-1}$
Preferences with regard to attributes of the fishing experience						
PWU of daily catch rate for an angler of type j	$U_{cj} = u_{5j}c_D + u_{6j}c_D^2$ (eqs. 1*a* and 1*b*), where c_D is the relative daily catch rate[c]; dome-shaped quadratic function: greater utility is gained from increasing catch rates (2, 3, 15) but marginal benefits decrease at high catch rates due to the lack of challenge (1, 2, 9)	As specialization increases: focus shifts from quantity to quality and to the challenge of the catch (2, 6, 15)	Intermediate interest in catch, lowest interest in challenge: u_{5j} = 0.968, u_{6j} = –0.121	Highest interest in catch, intermediate interest in challenge: u_{5j} = 1.318, u_{6j} = –0.220	Lowest interest in catch, highest interest in challenge: u_{5j} = 0.825, u_{6j} = –0.206	u_{5j} = 1.030, u_{6j} = –0.176

Table 3 (*continued*).

Variable	Symbol and defining equation (affected equation); rationale for general shape (source)	Rationale for angler-type-specific shape (source)	Parameters values describing angler types			
			Generic	Consumptive	Trophy	Average
PWU of average size of fish captured annually for an angler of type j	$U_{sj} = u_{7j}\bar{l} + u_{8j}$ (eq. 1*b*), where $\bar{l}$ is the relative size of fish caught[c]; linear function: anglers have a general preference for catching larger fish (2, 10, 11)	As specialization increases: importance attached to the size of fish increases (2, 6, 10)	Lowest: u_{7j} = 2.476, u_{8j} = 0.000	Intermediate: u_{7j} = 3.389, u_{8j} = 0.000	Highest: u_{7j} = 4.394, u_{8j} = –0.220	u_{7j} = 3.326, u_{8j} = –0.066
PWU of maximum size of fish captured annually for an angler of type j	$U_{xj} = \begin{cases} u_{9j}l_x & \text{if } l_x \geq 0 \\ -u_{9j}l_x & \text{if } l_x < 0 \end{cases}$ (eq. 1*b*), where l_x is the relative maximum size (= the 95th percentile in the size distribution of fish caught[c]); piecewise quadratic function: increasing when the relative maximum size[c] is positive and decreasing when it is negative; anglers gain greater utility from larger fish (18) and the relative value of large-sized fish is nonlinear (12)	As specialization increases: utility gained from large-sized fish increases (2, 6, 17) but the least specialized, generic anglers gain more utility than consumptive anglers in the unlikely event that they catch a large fish (8)	Intermediate: u_{9j} = 9.414	Lowest: u_{9j} = 6.878	Highest: u_{9j} = 12.207	u_{9j} = 9.491
PWU of crowding for an angler of type j	$U_{aj} = u_{10j}A + u_{11j}A^2 + u_{12j}$ (eq. 1*b*), where A is the expected daily congestion[d]; dome-shaped quadratic function: anglers gain utility from the social aspects of fishing but avoid congested sites (22)	As specialization increases: desire for solitude increases (6, 7, 22); consumptive anglers recognize that areas with high catch rates will attract other anglers (13)	Highest: u_{10j} = 0.244, u_{11j} = –0.031, u_{12j} = 0.610	Intermediate: u_{10j} = 0.149, u_{11j} = –0.025, u_{12j} = 0.396	Lowest: u_{10j} = 0.136, u_{11j} = –0.034, u_{12j} = 0.712	u_{10j} = 0.183, u_{11j} = –0.030, u_{12j} = 0.577
Fishing practices						
Skill level of an angler of type j	q_j (eq. 7*b*); measured in terms of catchability	As specialization increases: skill level increases (8, 10)	Lowest: q_j = 0.011 ha·h^{-1}	Intermediate: q_j = 0.020 ha·h^{-1}	Highest: q_j = 0.025 ha·h^{-1}	q_j = 0.018 ha·h^{-1}
Size selectivity for an angler of type j	y_j and z_j (eq. 7*a*); measured in terms of parameters for the size-dependent vulnerability to capture (modified from 20)	As specialization increases: type of fishing gear used changes (2, 6) and gear used by more specialized anglers catches larger fish (21)	Small: y_j = 0.21 cm^{-1}, z_j = 406	Small: y_j = 0.21 cm^{-1}, z_j = 406	Large: y_j = 0.21 cm^{-1}, z_j = 4636	y_j = 0.21 cm^{-1}, z_j = 1675

Can. J. Fish. Aquat. Sci. Vol. 67, 2010

Published by NRC Research Press

Table 3 (*concluded*).

Variable	Symbol and defining equation (affected equation); rationale for general shape (source)	Rationale for angler-type-specific shape (source)	Parameters values describing angler types			
			Generic	Consumptive	Trophy	Average
Threshold for practicing voluntary catch-and-release fishing for an angler of type j	c_{maxj} (eq. 7*e*); measured in terms of the desired average number of fish an angler will harvest daily	As specialization increases: propensity to harvest fish decreases (6)	Highest: $c_{maxj} = 2$	Lowest: $c_{maxj} = \infty$	Intermediate: $c_{maxj} = 0.5$	$c_{maxj} = \infty$
Hooking mortality for an angler of type j	f_{hj} (eqs. 7*f* and 7 *g*); measured in terms of the proportion of fish dying from hooking mortality	As specialization increases: no differences in hooking mortality levels (5) were assumed	$f_{hj} = 0.05$	$f_{hj} = 0.05$	$f_{hj} = 0.05$	$f_{hj} = 0.05$
Noncompliance mortality for an angler of type j	f_{nj} (eq. 7*c*); measured in terms of the proportion of fish under the MSL that are harvested illegally	As specialization increases: no differences in noncompliance were assumed; because values reported in the literature vary widely (19, 23, 24), a conservative constant value of 5% was assumed	$f_{nj} = 0.05$	$f_{nj} = 0.05$	$f_{nj} = 0.05$	$f_{nj} = 0.05$

Note: Source: 1, Aas and Kaltenborn 1995; 2, Aas et al. 2000; 3, Arlinghaus 2006*b*; 4, Arlinghaus and Mehner 2004*b*; 5, Arlinghaus et al. 2008*c*; 6, Bryan 1977; 7, Connelly et al. 2001; 8, Dorow et al. 2010; 9, Fedler and Ditton 1994; 10, Fisher 1997; 11, Gillis and Ditton 2002; 12, Jacobson 1996; 13, Martinson and Shelby 1992; 14, Massey et al. 2006; 15, Oh and Ditton 2006; 16, Oh et al. 2005*a*; 17, Oh et al. 2005*b*; 18, Paulrud and Laitila 2004; 19, Pierce and Tomcko 1998; 20, Post et al. 2003; 21, Rapp et al. 2008; 22, Schuhmann and Schwabe 2004; 23, Sullivan 2002; 24, Walker et al. 2007. Parameters describe four angler types (generic, consumptive, trophy, and average) in terms of the basic utility they gain from fishing, their tolerances with regard to managerial constraints, their preferences with regard to attributes of the fishing experience, and their fishing practices. Parameter values for the average angler type are weighted averages of the corresponding parameter values for the three prototypical angler types weighted by the proportion of each angler type in the angler population (40% generic, 30% consumptive, and 30% trophy). Parameter values for the angler-type-specific part-worth-utility (PWU) functions (Fig. 3) were chosen based on assumptions about differences among angler types reported in the angler-specialization literature. Figure 1 illustrates qualitative differences in angler preferences and Fig. 3 illustrates the angler-type-specific utility functions based on the parameters listed here.

[a] $r = \text{MSL}/L_{max}$ is the relative minimum-size limit standardized to range between 0 and 1, where L_{max} is the maximum size that a fish can attain at the maximum age allowed in the absence of density dependence (eqs. 4*a*–4*d*).

[b] $o = (O_o - O_e)$ is the annual fishing license cost relative to a baseline expected value, where O_o and O_e and are the observed and expected values, respectively.

[c] Attributes related to the fish population represent the proportional difference scaled relative to a baseline expected value as follows: $c_D = C_{Do}/C_{De} - 1$, where C_{Do} and C_{De}, respectively, are the observed and expected average daily catch rates, $\bar{l} = \bar{L}_o/\bar{L}_e - 1$, where $\bar{L}_o$ and $\bar{L}_e$, respectively, are the observed and expected average sizes of caught fish in a year, and $l_x = L_{xo}/L_{xe} - 1$, where L_{xo} and L_{xe}, respectively, are the observed and expected the maximum sizes of caught fish in a year (with the latter defined as the 95th percentile of the size distribution of caught fish). Expected values are based on the literature and on unpublished data from pike fisheries. We assumed an expected daily catch rate of 0.5 fish (Kempinger and Carline 1978; Goeman et al. 1993; Arlinghaus et al. 2008*c*) and that anglers fished 4 h in an angling day, an expected average size of 51 cm (Kempinger and Carline 1978; Pierce et al. 1995 (harvested fish); Arlinghaus et al. 2008*c*), and an expected average maximum size of 69 cm (M. Dorow and R. Arlinghaus, unpublished data).

[d] $A = \sum_j (D_j A_j)/(365 S_F)$ is the expected average number of anglers fishing in a day (eqs. 2*c*–2*d*).

Published by NRC Research Press

Table 4. Predicted optimal regulations and their implications.

	Angler population				
Scenario	Generic	Consumptive	Trophy	Average	Mixed
Optimal minimum-size limit (cm)					
Static, TU	80	53	99	69	69
Catch-based, TU	104	102	101	106	98
Multi-attribute, TU (EU, RU)	80	53	99	69	93 (69, 63)
Optimal angler-license number					
Static, TU	38	27	36	31	36
Catch-based, TU	92	100	99	100	100
Multi-attribute, TU (EU, RU)	52	36	39	44	66 (48, 48)
Annual realized angling effort under optimal regulations ($h \cdot ha^{-1}$)					
Static, TU	61	43	58	50	58
Catch-based, TU	80	112	93	94	97
Multi-attribute, TU (EU, RU)	61	43	58	50	65 (57, 57)
Composition of anglers fishing in the mixed angler population under optimal regulations					
Static, TU	0.40	0.30	0.30	na	na
Catch-based, TU	0.34	0.37	0.29	na	na
Multi-attribute, TU (EU, RU)	0.41 (0.38, 0.37)	0.14 (0.27, 0.29)	0.45 (0.35, 0.34)	na	na
Spawning-potential ratio under optimal regulations					
Static, TU	0.74	0.38	0.73	0.61	0.57
Catch-based, TU	0.78	0.54	0.61	0.67	0.63
Multi-attribute, TU (EU, RU)	0.74	0.39	0.73	0.61	0.73 (0.57, 0.48)

Note: Optimal input and output regulations maximized social welfare for various angler types and for different assumptions about angler-behaviour and social-welfare measures. Implications are shown in terms of resulting angling efforts and biological impacts (with the latter being measured by the spawning-potential ratio). Three social-welfare measures were examined for the mixed angler population: total utility (TU), an equitable utilitarian utility (EU), and a Rawlsian utility (RU) (Table 1, eqs. 8*a*–8*c*). For the nonmixed angler populations, results for the EU and RU were identical to those for TU and are therefore not repeated. na, not applicable.

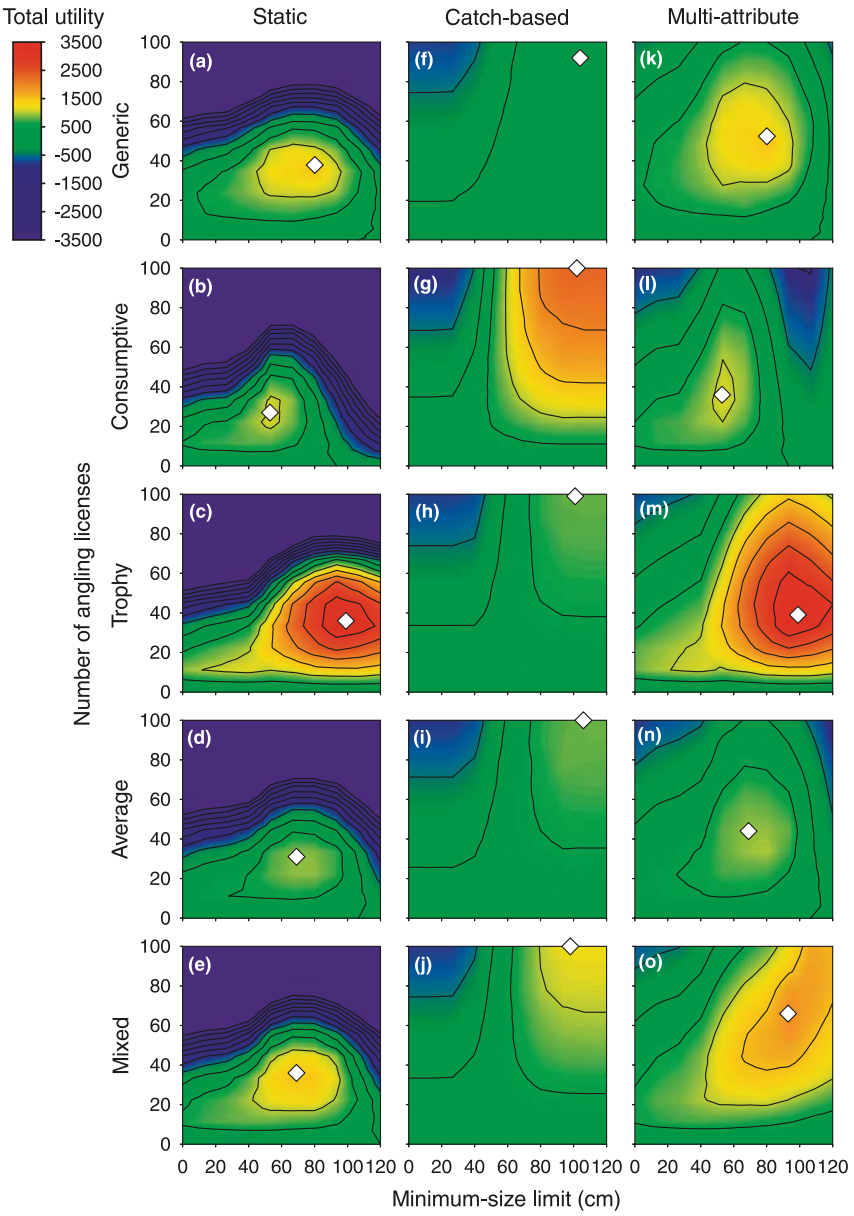
optimal regulations, the number of hours that anglers actually fished, termed realized angling effort, were identical in the static and multi-attribute scenarios when the angling population was composed of one angler type (thus following the pattern of predictions for optimal minimum-size limits). In the catch-based scenario, realized effort followed a trend similar to that of optimal license numbers.

The risk of recruitment overfishing and the biological impacts of recreational angling on the modelled pike population were affected by the type of angler behaviour considered (Fig. 5). Static angler behaviour caused the most negative impacts on the fish population across the range of minimum-size limits and license numbers examined compared with the two scenarios in which anglers behaved dynamically. This was because realized angling effort in the static angler-behaviour scenario was fixed at the maximum level allowed, whereas in the two dynamic scenarios, realized angling effort was less and depended on the utility anglers gained from the fishery. When comparing the two dynamic scenarios, biological impacts of fishing at low to moderate minimum-size limit levels in the catch-based scenario were generally less severe than in the multi-attribute scenario, with the latter approaching recruitment overfishing and fishery collapse at lower license numbers. At high minimum-size limit levels, approaching complete catch-and-release conditions, the risk of recruitment overfishing was often greater in the catch-based scenario, although the spawning-potential ratio never dropped below 0.4, even when a large number of licenses were issued.

Impacts of angler heterogeneity

Not only angler dynamics but also angler heterogeneity substantially affected model-predicted optimal input and output regulations. When the three angler types were compared (first three rows in Fig. 4), optimal minimum-size limits were generally intermediate for generic anglers, low for consumptive anglers, and high for trophy anglers, with the latter approaching complete catch-and-release conditions, except in the catch-based scenario in which complete catch-and-release regulations were preferred by all angler types (Fig. 4; Table 4). Optimal effort regulations were found to be the lowest for consumptive anglers in the static and multi-attribute scenarios, intermediate for trophy anglers, and highest for generic anglers. However, in the catch-based scenario, all angler types preferred a large number of licenses, with generic anglers favouring fewer angler licenses than the other angler types. Under optimal regulations, consumptive anglers were predicted to fish the least, but generic and trophy anglers invested more (and similar) realized angling efforts in the static and multi-attribute scenarios (Table 4). However, in the catch-based scenario, consumptive anglers invested the most realized angling effort. At their optimum, trophy anglers, as a homogeneous group, derived the highest utility from fishing, exceeding that of the

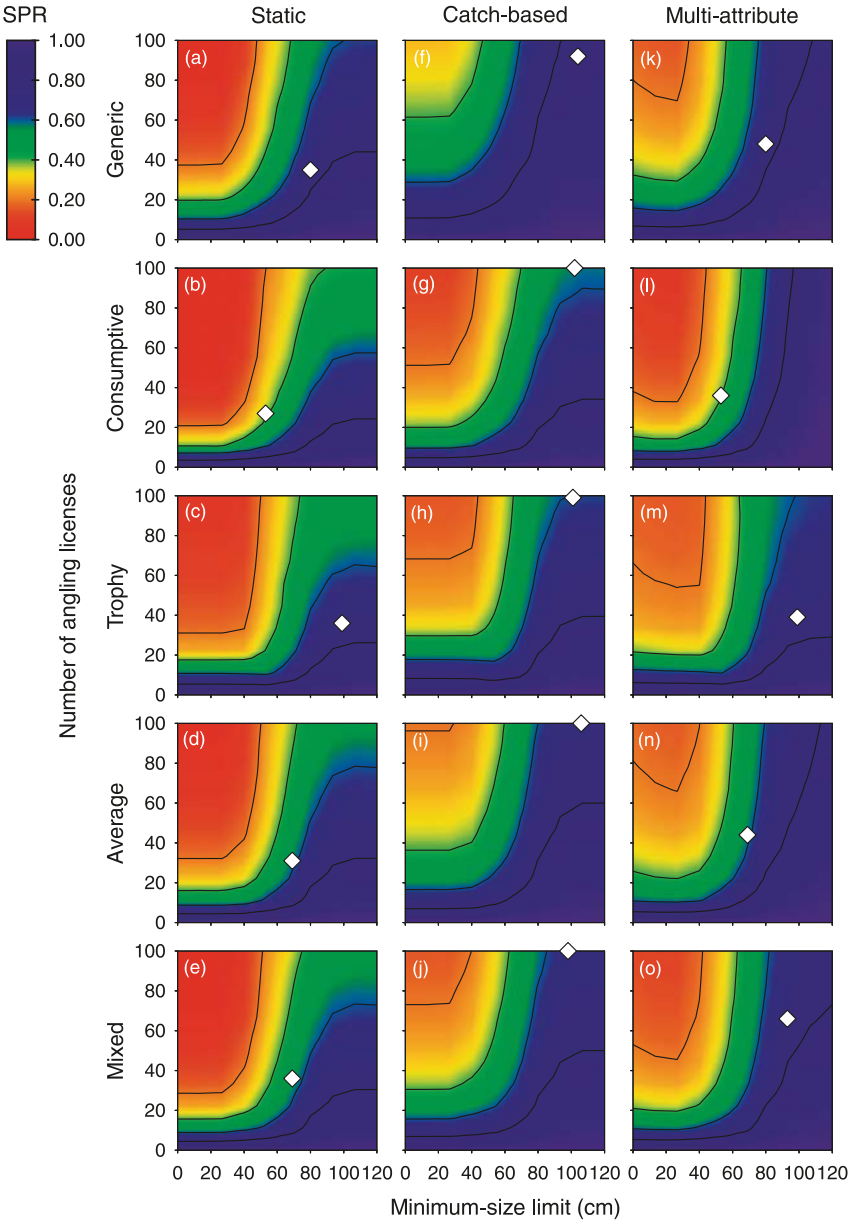
Fig. 4. Total utility over a range of input (license number) and output (minimum-size limit) regulations. Columns illustrate results for three angler-behaviour scenarios: static angler behaviour, where anglers fished at the maximal rate catch-based dynamic angler behaviour, where anglers responded to the fishery based on catch rates, and multi-attribute dynamic angler behaviour, where anglers responded to the fishery based on a multi-attribute utility function. Rows illustrate results for five different angler populations: generic anglers, consumptive anglers, trophy anglers, average anglers, and a mixed angler population composed of 40% generic, 30% consumptive, and 30% trophy anglers. White diamonds indicate the optimum regulations at which total utility was maximized.



other anglers types by a factor of more than 2; generic anglers were intermediate, while consumptive anglers derived the least utility in the static and multi-attribute scenarios (Fig. 4).

Differences among the angler types also affected the risk of recruitment overfishing. In all scenarios and across all regulation combinations, consumptive anglers generally had the most negative impact and generic anglers the least, except in the multi-attribute scenario at high minimum-size limits. This trend was also seen when examining the biological impacts of different angler types under the different regulations they perceived as optimal (Table 4). Under these

Fig. 5. Spawning-potential ratio (SPR) of fished populations over a range of input (license number) and output (minimum-size limit) regulations. SPR values below 0.35–0.4 indicate a potential for recruitment overfishing. Columns show results for three angler-behaviour scenarios: static angler behaviour, where anglers fished at the maximal rate, catch-based dynamic behaviour, where anglers responded to the fishery based on catch rates, and multi-attribute dynamic behaviour, where anglers responded to the fishery based on a multi-attribute utility function. Rows show results for five different angler populations: generic anglers, consumptive anglers, trophy anglers, average anglers, and a mixed angler population composed of 40% generic, 30% consumptive, and 30% trophy anglers. White diamonds indicate the optimum regulations at which total utility was maximized.



optimal regulations, the biological impact of consumptive anglers was greatest, occurring close to the threshold levels of recruitment overfishing (0.35–0.40) and at regulation combinations for which small changes in regulations could cause large changes in the risk of recruitment overfishing (Fig. 5). At these respective optima, generic and trophy anglers impacted the fish population much less than consumptive anglers and regulation combinations implied a low risk of recruitment overfishing.

We found that the sensitivity of results to individual at-

Fig. 6. Proportion of the total realized angling effort contributed by each angler type, (*a*) generic, (*b*) consumptive, and (*c*) trophy, in a mixed angler population over a range of input (license number) and output (minimum-size limit) regulations. The mixed angler population was composed of 40% generic, 30% consumptive, and 30% trophy anglers. Anglers responded to the fishery based on a multi-attribute utility function; see Figs. 4*o* and 5*o*. White diamonds indicate the optimum regulations at which total utility was maximized.

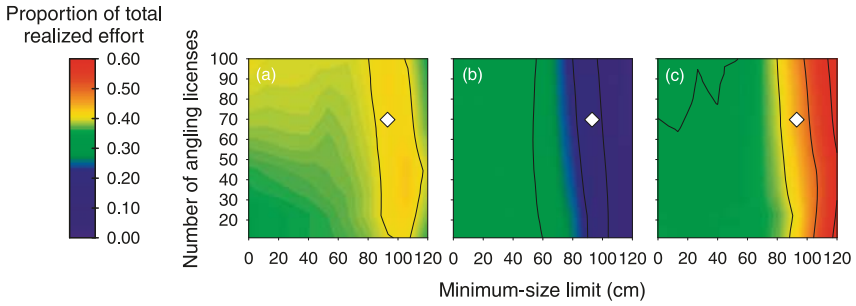
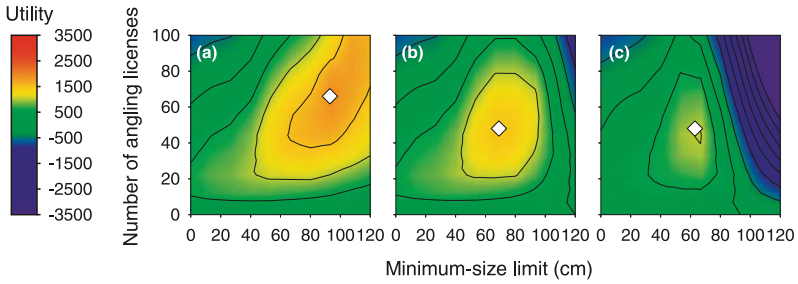


Fig. 7. Social-welfare measures in a mixed angler population with multi-attribute dynamic angler behaviour over a range of input (license number) and output (minimum-size limit) regulations. The mixed angler population was composed of 40% generic, 30% consumptive, and 30% trophy anglers. Results are shown for three social-welfare measures, (*a*) total utility (TU), (*b*) egalitarian utilitarian utility (EU), and (*c*) Rawlsian utility (RU) (see Table 1, eqs. 8*a*–8*c*). White diamonds indicate the optimum regulations at which the social-welfare measures were maximized.



tributes in the multi-attribute scenario varied in their effect on optimal regulations, realized effort, and spawning-potential ratio and varied greatly with angler type, without any consistent pattern becoming evident (Appendix A). We could tentatively conclude, however, that findings for trophy anglers were strongly dependent on crowding aversion, while findings for consumptive anglers were particularly sensitive to minimum-size limit levels and some catch attributes. It was also interesting to notice that the response of mixed angler populations to the removal of a particular fishery attribute sometimes exceeded that of homogeneous angler populations, highlighting the importance of including heterogeneity in angler preferences (Appendix A).

Impacts of angler-population composition

Predictions of optimal input and output regulations substantially differed between the average angler and the mixed angler population (bottom two rows in Fig. 4). Under optimal regulations, license numbers and realized angling efforts were higher for the mixed angler population than for the average angler population (Table 4). Optimal minimum-size limits for the mixed angler population were the same as for the average angler population in the static scenario, lower in the catch-based scenario, and higher in the multi-attribute scenario. In addition, across all scenarios, total utility under optimal regulations was greater in the mixed angler population than in the average angler population.

For the average angler population, minimum-size limits and realized efforts under optimal regulations were identical in the static and multi-attribute scenarios. However, for the mixed angler population, minimum-size limits, license numbers, and realized efforts under optimal regulations were substantially higher in the multi-attribute scenario than in the static scenario (Fig. 4; Table 4). Furthermore, in the multi-attribute scenario, predictions of optimal license sales and realized efforts were generally higher than in any of the three homogeneous angler populations (Table 4). The mixed angler population was also predicted to have a greater biological impact than the average angler population (Fig. 5). However, under optimal regulations, the risk of recruitment overfishing in both cases was low (Table 4).

Changes in the composition of the mixed angler population that fished in the multi-attribute scenario were described by the changes in the proportion of total realized angling effort invested by each angler type (Fig. 6). This shows that the composition of the angling population varied depending on minimum-size limits and license regulations, with trends predominantly following changes in minimum-size limit (Fig. 6). At low minimum-size limits and low license numbers, all angler types fished in approximately equal propor-

tions, whereas at low minimum-size limits and high license numbers, the composition of the angling population resembled that of the entire angler population (i.e., 40% generic, 30% consumptive, and 30% trophy). At moderate to high minimum-size limits, the majority of consumptive anglers in the angler population chose not to fish and thus dropped out of the angling population. Even higher minimum-size limits resulted in generic anglers also dropping out resulting in an angling population dominated by trophy anglers. Under optimal regulations, the composition of the angling population in the multi-attribute scenario was heavily skewed toward generic and trophy anglers, with few consumptive anglers being attracted to the fishery (Table 4; Fig. 6).

Impacts of social-welfare measures

In the multi-attribute scenario for the mixed angler population, socially optimal minimum-size limits were highest for total utility, intermediate for equitable utilitarian utility, and lowest for Rawlsian utility (Fig. 7; Table 4). Optimal license numbers were also highest for the total utility social-welfare measure but lower (and similar) for the equitable utilitarian utility and the Rawlsian-utility social-welfare measures. Realized angling efforts under optimal conditions showed the same pattern.

Under optimal regulations, optimal license numbers and realized angling efforts for the average angler population never exceeded those for the mixed angler population, irrespective of the applied social-welfare measure (Table 4). However, the optimal minimum-size limit was slightly higher in the average angler population than in the mixed population when the Rawlsian-utility social-welfare measure was applied (Table 4). Under optimal regulations, spawning-potential ratio levels were well above 0.40, irrespective of the applied social-welfare measure (Table 4); therefore, all social-welfare measures avoided recruitment overfishing under optimal regulations.

Discussion

We developed a bioeconomic modelling approach that integrates angler behaviour and angler heterogeneity with age-structured and density-dependent fish population dynamics to determine socially optimal input and output regulations for a recreational fishery. Using this approach, we have demonstrated how angler behaviour and heterogeneity affect optimal regulations and how optimal regulations varied with the social-welfare measure applied.

Angler behaviour

The importance of accounting for angler behaviour was demonstrated by the differences observed in predicted optimal regulations (expressed in terms of minimum-size limits and license numbers) among three angler-behaviour scenarios that describe, respectively, static, catch-based, and multi-attribute angling dynamics. Predicted optimal minimum-size limits and license numbers were substantially higher for the catch-based scenario than for the other two scenarios. However, most published recreational-fisheries models that incorporated dynamic angler behaviour assumed that anglers respond to catch rates alone or to some measure of fish abundance (Johnson and Carpenter 1994; Beard et al. 2003; Post et al. 2003), thus neglecting other attributes known to affect participation decisions of anglers (Hunt 2005).

Our findings call into question the validity of this simplifying assumption and resulting predictions of "optimal" regulations. For example, when catch rate was assumed to be the only attribute determining the fishing decisions of anglers, the catch-based scenario predicted optimal input and output regulations that effectively imply complete catch-and-release regulatory policies at largely unlimited effort levels. This prediction is clearly misleading in many situations and results from an oversimplification of angler preferences. Indeed, because some angler types are strongly harvest oriented, management conflicts and dilemmas have occurred in some recreational fisheries despite high catch rates when the possibility for anglers to harvest was constrained (Matlock et al. 1988; Radomski 2003; Sullivan 2003). Perceived harvest constraints may result in the displacement of harvest-oriented anglers to alternative fisheries (Radomski and Goeman 1996; Beard et al. 2003), an important effect that cannot be captured by models that assume angler behaviour to be driven by catch rates alone. In contrast, our investigations of multi-attribute dynamic angler behaviour, presumably allowing a more realistic representation of angling effort, showed that complete catch-and-release regulations were not always socially optimal.

Our sensitivity analyses highlighted that, while most attributes of the fishing experience (such as fish size, catch rate, crowding, aversion to regulations, etc.) were important for determining angler choice and angler welfare, their relative importance varied among angler types (Appendix A). This underscores the importance of including all relevant catch- and non-catch-related attributes affecting angler choice in bioeconomic fisheries models to more accurately predict angler behaviour and fishing pressure and to derive optimal regulations that maximize angler welfare.

A multi-attribute perspective on angler behaviour and welfare is also likely to improve predictions of the biological impacts of fishing under different regulations. Historically, angler populations were expected to be self-regulating, as anglers were assumed to leave a fishery when catch rates declined (Cox and Walters 2002*a*; Radomski 2003). However, because catch rate is just one among many attributes characterizing a fishing experience, such catch-based self-regulation does not necessarily apply (Post et al. 2002, 2008; Paulrud and Laitila 2004). Indeed, we found that realized angling effort and the biological impacts were higher in the multi-attribute scenario than in the catch-based scenario at low to intermediate minimum-size limits. These findings corroborate claims that multi-attribute angler behaviour may put fish populations at risk of overexploitation (Post et al. 2002), since anglers continue to be attracted to particular fisheries even after catch rates have declined, because other attributes of the fishery (such as close proximity or social aspects of the experience) provide them with utility and thereby partly compensate for reduced catch rates. The interesting features of the multi-attribute utility scenario derive from its partial "decoupling" of fish and angler dynamics (Johnson and Carpenter 1994). In contrast, the catch-based scenario is appropriate for describing predator–prey interac-

tions if a predator's fitness is predominantly dependent on prey consumption. Not accounting for the array of attributes that attract anglers to a fishery may therefore lead to an underestimation of the biological impacts of fishing (Post et al. 2002). Consequently, management decisions based on assumptions of purely catch-based angler behaviour will likely be less conservative than intended with regard to limiting biological impacts and probably also less successful than intended with regard to angler satisfaction and participation.

Angler heterogeneity

Our results have shown that accounting for the complexity of angler behaviour when predicting the amount of angling effort invested in a particularly fishery can fundamentally improve predictions about optimal regulations. However, this improvement alone might not be enough: predictions are likely even more realistic when the heterogeneity of angler behaviour is considered in recreational-fisheries models.

We found that, because of the consumptive orientation and aversion to angling regulations of some angler types, minimum-size limits were particularly important in determining angler utility and optimal regulations. Under less restrictive output regulations, consumptive angling effort was reduced because the fish population could not support large numbers of harvest-oriented anglers while at the same time maintaining high catch rates. In these situations, trophy anglers fished in greater numbers than consumptive anglers because they were less concerned with harvest constraints and more interested in attributes of the fishery unrelated to catch rates. Despite their greater numbers, at low minimum-size limits, the less consumptive nature and the reduced catch rates of trophy anglers (which occurred because they used gear that targeted fish of larger size) resulted in them imposing less fishing mortality on a fish stock than consumptive anglers.

This demonstrates that both aspects of angler heterogeneity, diversity in angling preferences and differences in fishing practices, are important when determining optimal angling regulations. Furthermore, while managing for angler diversity to enhance the recreational-fishing experience of all anglers has been repeatedly called for (Driver et al. 1984; Aas et al. 2000; Arlinghaus and Mehner 2004*a*), our study is the first to explicitly demonstrate the benefits of such an approach when determining optimal, angler-type-specific regulations to maximize social welfare.

Although the aim of our modelling exercise was to explore the general importance of behavioural complexity and diversity in anglers, our model-based results also highlight some practical implications. In particular, our model findings suggest that some minimum-size limit regulations currently used for pike fisheries (45–75 cm in North America; Paukert et al. 2001) are below the optimal levels (53–99 cm) predicted by our model for the different angler types. Implementation of lower-than-optimal minimum-size limits could put fish populations at risk of recruitment overfishing (e.g., Arlinghaus et al. 2010). Thus, depending on the composition of the local angler population, special regulations described by Paukert et al. (2001) that are geared toward particular angler types (e.g., maximum-size limits and inverse slot length limits) may perform better than the standard solution of imposing a moderately low minimum-size limit (such as 45–50 cm).

Despite considerable differences among angler types, we found that socially optimal regulations resulted in biologically sustainable exploitation patterns. This is because angler utility is partly dependent on catch-related attributes of the fishery (such as catch rates or fish size), which implicitly requires a productive, biologically sustainable fishery in the long term. Our results therefore indicate that socioeconomic management objectives, such as maximizing social welfare, can account for the state of a fish population through its influence on angler utility and thus provide management advice that results in biologically sustainable exploitation. This supports suggestions for a focus on OSY when managing for sustainability (Roedel 1975; Malvestuto and Hudgins 1996; Carpenter and Brock 2004). However, the occurrence of optimal regulations in the vicinity of spawning-potential ratio levels suggestive of recruitment overfishing varied with angler type. Thus, a precautionary approach has to be taken in socially optimal management to account for the stochastic processes underlying any fishery.

Angler-population composition

The results discussed so far account for the dynamics and heterogeneity in angler behaviour. However, they are still limited in the sense that the angler population was assumed to be composed of just one angler type. In reality, angler populations are composed of different types of anglers that vary in their preferences and behaviour (Hahn 1991; Fisher 1997; Connelly et al. 2001). Our study has shown that this composition affects optimal regulations. Moreover, while managers might be inclined, for the sake of simplicity, to represent angler populations in terms of an average angler (Hahn 1991; Aas and Ditton 1998), we found that such a simplification can lead to misleading predictions of optimal regulations and biological impacts. This is because different angler types dominated the realized angling effort under different regulations and because optimal regulations were consistently more restrictive for the mixed angler populations than for the average populations. Shifts in the angling population were also important for determining biological impacts because of differences in fishing practices and participation of the different angler types.

Therefore, our model results underscore the importance of considering not only dynamic angler behaviour and angler heterogeneity in both angling preferences and angling practices in models of recreational-fisheries management (Post et al. 2008), but also how dynamics and diversity interact in angler populations containing a mixture of angler types. Our findings suggest that current monitoring methods that pool information about anglers need to be modified to account for the heterogeneity of angler types using specific fisheries. This will allow managers to understand better which types of anglers are fishing and why (Radomski et al. 2001), thus yielding insights that our model results suggest could be of crucial importance for determining optimal regulations and for more accurately predicting the biological impacts of the angling population.

Social-welfare measures

A final insight from this study relates to the importance of

the management objectives determining optimal input and output regulations. From a welfare-economics perspective, the management objective is to maximize the social welfare a fishery provides to the angling community irrespective of which anglers benefit the most or the least (Cole and Ward 1994; Perman et al. 2003). However, our results suggest that a strictly utilitarian economic approach may alienate some angling groups from a fishery that is managed for maximum total utility. For example, we found that consumptive anglers interested in fish harvest were no longer attracted to a fishery that was subject to restrictive minimum-size limits. Trophy anglers, in contrast, enjoyed high individual utility at high minimum-size limits, mainly because of their lack of consumptive orientation and the greater importance of fishing to their lifestyle. As a result, trophy anglers gained more utility, which strongly influenced the total utility social-welfare measure, and thus optimal regulations. Social-welfare measures that reflected more equitable management objectives, such as equitable utilitarian utility or Rawlsian utility, rendered optimal regulations in mixed angler populations more restrictive but resulted in a more diverse composition of anglers attracted to a fishery.

Thus, although there is no universal consensus about which social-welfare functions to use to quantify welfare (Cole and Ward 1994; Perman et al. 2003), our results illustrate how the optimal regulations predicted by bioeconomic models are sensitive to the social-welfare measures applied. Therefore, managers need to be explicit about their underlying management goals and objectives (Barber and Taylor 1990; Aas and Ditton 1998) and ensure that the welfare measure applied closely reflects these objectives when implementing an OSY approach to recreational-fisheries management.

Limitations and extensions

While we hope that our study provides valuable insights about the importance of angler dynamics and angler heterogeneity when managing for OSY, several limitations need to be highlighted. First, our model results depend on the description of angler behaviour. Application of our modelling approach to local fisheries therefore requires a quantitative assessment of the local and regional angler populations, e.g., using stated and revealed choice models (Hunt 2005; Massey et al. 2006). A second limitation is that we assumed that over time, anglers will follow the same behavioural patterns and will keep occurring in the same proportions, which may be in error (Baerenklau and Provencher 2005). Temporal trends in the behaviour of individual anglers or in the composition of the angler population could be examined in future extensions of our model. Changing preferences of anglers over time due to specialization or learning could also be exciting to investigate, as anglers will likely adapt to changes in a fishery by altering their expectations (Arlinghaus 2006*a*). Third, to simplify an already complex model, we assumed that participation decisions were made on an annual basis, whereas other time steps may be more realistic (Schuhmann and Schwabe 2004; Hunt 2005). However, because we were interested in long-term equilibrium conditions, this simplifying assumption seems warranted. Fourth, our model described a single fishery and therefore did not account for changes in utility offered by substitute sites in the vicinity of the modelled fishery. Clearly, this is an unrealistic assumption, and further research is needed to broaden our modelling approach to fisheries landscapes (Lester et al. 2003).

A final limitation of this study is that we defined social welfare in terms of aggregated utility rather than aggregated willingness-to-pay. In environmental and resource economics, including recreational-fisheries economics, an aggregate of individuals' willingness-to-pay for an environmental good or service is a commonly used welfare measure (Edwards 1991). In empirical studies of nonmarketable goods and services, such as recreational fisheries, this measure of social welfare is calculated using the change in utility provided by attributes of the good (such as catch rate or crowding) from one condition of the fishery to another divided by the marginal utility of income (such as the license cost coefficient in our model) and is expressed in monetary units (Hanemann 1984). Here, we chose not to express utility in monetary units because this would necessitate making an additional assumption about the baseline condition used for comparison and because it was felt to be imprudent to put a monetary value on hypothetical scenarios. However, such calculations could be carried out if appropriate empirically derived parameters were available from stated- or revealed-preference models for angler-type-specific part-worth-utility functions (e.g., Massey et al. 2006). This would also ensure that the welfare measure has a cardinal scale, thus avoiding the potential debate of how comparable utility is among individuals (Perman et al. 2003).

Despite these limitations, by coupling socioeconomic and biological models, our modelling framework is among the few that address the often-touted need for an interdisciplinary approach to recreational-fisheries management (e.g., Anderson 1993; Johnson and Carpenter 1994; Radomski et al. 2001), thus providing a basis for future research. There are numerous directions in which our model can be extended, including incorporating environmental stochasticity and a multispecies biology. These extensions are important because deterministic models (Carpenter et al. 1994) and single-species models (Worm et al. 2009) may result in erroneous conclusions about appropriate management strategies. In multispecies models, incorporating angling preferences for different species and indirect effects of angling on the aquatic food webs (Roth et al. 2007) are promising options for complementing the predictions presented here.

Further avenues for future research include exploring the part-worth-utility functions driving angler behaviour, examining the sensitivity of model predictions to changes in fishery attributes, and investigating an even larger number of prototypical angler types and their interactions in mixed angling populations. Because multilake fisheries opportunities (Parkinson et al. 2004; Post et al. 2008) are more realistic than the simplified single-lake perspective we have adopted here, exploration of angler choice within a landscape of fishing opportunities (Carpenter and Brock 2004) may be the most important extension of our modelling approach.

Implications

Even though we have just scratched the surface, we hope that readers share our optimism that the interdisciplinary approach to modelling recreational fisheries introduced here

constitutes a sound and extensible theoretical framework. The approach builds on choice theory from welfare economics, angler-specialization theory from leisure sciences, and traditional ecological theory and provides unique insights into recreational-fisheries management.

A key finding of this study and related work (Carpenter and Brock 2004) is that "one-size-fits-all" policies are likely to produce suboptimal management outcomes because they cannot account for the diversity and complexity of angler behaviour that is inherent to most of the world's recreational fisheries (Cox et al. 2003; Arlinghaus et al. 2008*a*; Post et al. 2008). Furthermore, we have shown that misleading predictions about optimal management can result from the omission of dynamic angler behaviour and angler heterogeneity from recreational-fisheries models; this can put fish populations at risk of overfishing, in line with what has been suggested by other studies (Carpenter et al. 1994; Parkinson et al. 2004). In contrast, although managers need to be aware that socially optimal regulations strongly depend on the applied measure of social welfare and the management objectives upon which it is based, managing for socially optimal regulations resulted in both social and biological sustainability.

Managers are likely to encounter difficulties in jointly satisfying the interests of the entire angling public. Decisions therefore need to be made about how to best distribute access to scarce resources across angler types (Loomis and Ditton 1993; Daigle et al. 1996). The benefit of an interdisciplinary bioeconomic modelling approach is that it enables managers to quantify welfare changes resulting from alternative management scenarios and to predict how these regulations will affect different segments of the angling public as well as the fish population. A decision-support tool such as this one, built on clear objectives and quantitative descriptions, thereby fostering transparency and legitimacy in the management process, can facilitate decision taking and clarify when managing for diverse angling opportunities is the best strategy. Ideally, accounting for angler dynamics and angler diversity in fisheries-management models will provide more accurate and realistic predictions of optimal regulations that maximize angler satisfaction, minimize conflicts among angling groups, and result in the sustainable management of recreational fisheries.

Acknowledgments

We thank Ben Beardmore, Barbara Fischer, Brad Gentner, Wolfgang Haider, Len Hunt, and Shuichi Matsumura for advice during the development of this study. We are also indebted to two anonymous reviewers for constructive comments that helped us improve the clarity of this manuscript. Financial support for this research was provided by the Gottfried-Wilhelm-Leibniz Community through the Adaptfish Project (www.adaptfish.igb-berlin.de). R.A. received additional funding through the German Ministry for Education and Research through the Program for Social-Ecological Research within the Besatzfisch-Project (Vorhaben 01UU0907, www.besatz-fisch.de). U.D. gratefully acknowledges financial support from the European Commission through the Marie Curie Research Training Network on Fisheries-Induced Adaptive Changes in Exploited Stocks (FishACE, MRTN-CT-2004-005578) and the Specific Targeted Research Project on Fisheries-Induced Evolution (FinE, SSP-2006-044276) under the European Community's Sixth Framework Program. U.D. received additional support from the European Science Foundation, the Austrian Science Fund, the Austrian Ministry of Science and Research, and the Vienna Science and Technology Fund.

References

Aas, Ø., and Ditton, R.B. 1998. Human dimensions perspective on recreational fisheries management: implications for Europe. *In* Recreational fisheries: social, economic and management aspects. *Edited by* P. Hickley and H. Tompkins. Blackwell Scientific Publications, Oxford, U.K. pp. 153–164.

Aas, Ø., and Kaltenborn, B.P. 1995. Consumptive orientation of anglers in Engerdal, Norway. Environ. Manag. **19**(5): 751–761. doi:10.1007/BF02471957.

Aas, Ø., Haider, W., and Hunt, L. 2000. Angler responses to potential harvest regulations in a Norwegian sport fishery: a conjoint-based choice modeling approach. N. Am. J. Fish. Manag. **20**(4): 940–950. doi:10.1577/1548-8675(2000)020<0940:ARTPHR>2.0.CO;2.

Adamowicz, W., Louviere, J., and Williams, M. 1994. Combining revealed and stated preference methods for valuing environmental amenities. J. Environ. Econ. Manag. **26**(3): 271–292. doi:10.1006/jeem.1994.1017.

Allen, M.S., and Miranda, L.E. 1996. A qualitative evaluation of specialization among crappie anglers. Am. Fish. Soc. Symp. **16**: 145–151.

Allen, M.S., Brown, P., Douglas, J., Fulton, W., and Catalano, M. 2009. An assessment of recreational fishery harvest policies for Murray cod in southeast Australia. Fish. Res. **95**(2–3): 260–267. doi:10.1016/j.fishres.2008.09.028.

Anderson, L.G. 1993. Toward a complete economic theory of the utilization and management of recreational fisheries. J. Environ. Econ. Manag. **24**(3): 272–295. doi:10.1006/jeem.1993.1018.

Arlinghaus, R. 2006*a*. On the apparently striking disconnect between motivation and satisfaction in recreational fishing: the case of catch orientation of German anglers. N. Am. J. Fish. Manag. **26**(3): 592–605. doi:10.1577/M04-220.1.

Arlinghaus, R. 2006*b*. Overcoming human obstacles to conservation of recreational fishery resources, with emphasis on central Europe. Environ. Conserv. **33**(1): 46–59. doi:10.1017/S0376892906002700.

Arlinghaus, R. 2007. Voluntary catch-and-release can generate conflict within the recreational angling community: a qualitative case study of specialised carp, *Cyprinus carpio*, angling in Germany. Fish. Manag. Ecol. **14**(2): 161–171. doi:10.1111/j.1365-2400.2007.00537.x.

Arlinghaus, R., and Cooke, S.J. 2009. Recreational fisheries: socioeconomic importance, conservation issues and management challenges. *In* Recreational hunting, conservation and rural livelihoods: science and practice. *Edited by* B. Dickson, J. Hutton, and B. Adams. Blackwell Publishing, Oxford, U.K. pp. 39–58.

Arlinghaus, R., and Mehner, T. 2003. Management preferences of urban anglers: habitat rehabilitation versus other options. Fisheries, **28**(6): 10–17. doi:10.1577/1548-8446(2003)28[10:MPOUA]2.0.CO;2.

Arlinghaus, R., and Mehner, T. 2004*a*. A management-orientated comparative analysis of urban and rural anglers living in a metropolis (Berlin, Germany). Environ. Manag. **33**(3): 331–344. doi:10.1007/s00267-004-0025-x. PMID:15037955.

Arlinghaus, R., and Mehner, T. 2004*b*. Testing the reliability and construct validity of a simple and inexpensive procedure to mea-

sure the use value of recreational fishing. Fish. Manag. Ecol. **11**(1): 61–64. doi:10.1111/j.1365-2400.2004.00356.x.

Arlinghaus, R., Cooke, S.J., Lyman, J., Policansky, D., Schwab, A., Suski, C., Sutton, S.G., and Thorstad, E.B. 2007. Understanding the complexity of catch-and-release in recreational fishing: an integrative synthesis of global knowledge from historical, ethical, social and biological perspectives. Rev. Fish. Sci. **15**(1): 75–167. doi:10.1080/10641260601149432.

Arlinghaus, R., Johnson, B.M., and Wolter, C. 2008*a*. The past, present and future role of limnology in freshwater fisheries science. Int. Rev. Hydrobiol. **93**(4–5): 541–549. doi:10.1002/iroh.200711047.

Arlinghaus, R., Bork, M., and Fladung, E. 2008*b*. Understanding the heterogeneity of recreational anglers across an urban–rural gradient in a metropolitan area (Berlin, Germany), with implications for fisheries management. Fish. Res. **92**(1): 53–62. doi:10.1016/j.fishres.2007.12.012.

Arlinghaus, R., Klefoth, T., Kobler, A., and Cooke, S.J. 2008*c*. Size selectivity, injury, handling time, and determinants of initial hooking mortality in recreational angling for northern pike: the influence of type and size of bait. N. Am. J. Fish. Manag. **28**(1): 123–134. doi:10.1577/M06-263.1.

Arlinghaus, R., Matsumura, S., and Dieckmann, U. 2010. The conservation and fishery benefits of protecting large pike (*Esox lucius*) by harvest regulations in recreational fishing. Biol. Conserv. **143**(6): 1444–1459. doi:10.1016/j.biocon.2010.03.020.

Baccante, D. 1995. Assessing catch inequality in walleye angling fisheries. N. Am. J. Fish. Manag. **15**(3): 661–665. doi:10.1577/1548-8675(1995)015<0661:ACIIWA>2.3.CO;2.

Baerenklau, K.A., and Provencher, B. 2005. Static modeling of dynamic recreation behavior: implications for prediction and welfare estimation. J. Environ. Econ. Manag. **50**(3): 617–636. doi:10.1016/j.jeem.2005.03.001.

Barber, W.E., and Taylor, J.N. 1990. The importance of goals, objectives, and values in the fisheries management process and organization: a review. N. Am. J. Fish. Manag. **10**(4): 365–373. doi:10.1577/1548-8675(1990)010<0365:TIOGOA>2.3.CO;2.

Beard, T.D., Jr., Cox, S.P., and Carpenter, S.R. 2003. Impacts of daily bag limit reductions on angler effort in Wisconsin walleye lakes. N. Am. J. Fish. Manag. **23**(4): 1283–1293. doi:10.1577/M01-227AM.

Bennett, D.H., Hampton, E.L., and Lackey, R.T. 1978. Current and future fisheries management goals: implications for future management. Fisheries, **3**(1): 10–14. doi:10.1577/1548-8446(1978)003<0010:CAFFMG>2.0.CO;2.

Bryan, H. 1977. Leisure value systems and recreational specialization: the case of trout fishermen. J. Leisure Res. **9**(3): 174–187.

Carpenter, S.R., and Brock, W.A. 2004. Spatial complexity, resilience, and policy diversity: fishing on lake-rich landscapes. Ecol. Soc. **9**(1): 8 [online]. Available from www.ecologyandsociety.org/vol9/iss1/art8/.

Carpenter, S.R., Muñoz-del-Rio, A., Newman, S., Rasmussen, P.W., and Johnson, B.M. 1994. Interactions of anglers and walleyes in Escanaba Lake, Wisconsin. Ecol. Appl. **4**(4): 822–832. doi:10.2307/1942011.

Coggins, L.G., Jr., Catalano, M.J., Allen, M.S., Pine, W.E., III, and Walters, C.J. 2007. Effects of cryptic mortality and the hidden costs of using length limits in fishery management. Fish Fish. **8**(3): 196–210.

Cole, R.A., and Ward, F.A. 1994. Optimum fisheries management policy: angler opportunity versus angler benefit. N. Am. J. Fish. Manag. **14**(1): 22–33. doi:10.1577/1548-8675(1994)014<0022:OFMPAO>2.3.CO;2.

Connelly, N.A., Knuth, B.A., and Brown, T.L. 2001. An angler typology based on angler fishing preferences. Trans. Am. Fish. Soc. **130**(1): 130–137. doi:10.1577/1548-8659(2001)130<0130:AATBOA>2.0.CO;2.

Cox, S., and Walters, C. 2002*a*. Maintaining quality in recreational fisheries: how success breeds failure in management of open-access sport fisheries. *In* Recreational fisheries: ecological, economic and social evaluation. *Edited by* T.J. Pitcher and C.E. Hollingworth. Blackwell Publishing, Oxford, U.K. pp. 107–119.

Cox, S.P., and Walters, C. 2002*b*. Modeling exploitation in recreational fisheries and implications for effort management on British Columbia rainbow trout lakes. N. Am. J. Fish. Manag. **22**(1): 21–34. doi:10.1577/1548-8675(2002)022<0021:MEIRFA>2.0.CO;2.

Cox, S.P., Walters, C.J., and Post, J.R. 2003. A model-based evaluation of active management of recreational fishing effort. N. Am. J. Fish. Manag. **23**(4): 1294–1302. doi:10.1577/M01-228AM.

Craig, J.F., and Kipling, C. 1983. Reproduction effort versus the environment — case-histories of Windermere perch, *Perca fluviatilis* L., and pike, *Esox lucius* L. J. Fish Biol. **22**(6): 713–727. doi:10.1111/j.1095-8649.1983.tb04231.x.

Daigle, C.P., Loomis, D.K., and Ditton, R.B. 1996. Procedural justice in fishery resource allocations. Fisheries, **21**(11): 18–23. doi:10.1577/1548-8446(1996)021<0018:PJIFRA>2.0.CO;2.

Die, D.J., Restrepo, V.R., and Hoenig, J.M. 1988. Utility-per-recruit modelling: a neglected concept. Trans. Am. Fish. Soc. **117**(3): 274–281. doi:10.1577/1548-8659(1988)117<0274:UMANC>2.3.CO;2.

Ditton, R.B., Loomis, D.K., and Choi, S. 1992. Recreational specialization: re-conceptualization from a social worlds perspective. J. Leisure Res. **24**(1): 35–51.

Dorow, M., Beardmore, B., Haider, W., and Arlinghaus, R. 2010. Winners and losers of conservation policies for European eel (*Anguilla anguilla* L.): an economic welfare analysis for differently specialised eel anglers. Fish. Manag. Ecol. **17**(2): 106–125. doi:10.1111/j.1365-2400.2009.00674.x.

Driver, B.L., Phillips, C., Bergersen, E.P., and Harris, C.C. 1984. Using angler preference data in defining types of sport fisheries to manage. Trans. N. Am. Wildl. Nat. Resour. Conf. **49**: 82–90.

Dunlop, E.S., Shuter, B.J., and Dieckmann, U. 2007. Demographic and evolutionary consequences of selective mortality: predictions from an eco-genetic model for smallmouth bass. Trans. Am. Fish. Soc. **136**(3): 749–765. doi:10.1577/T06-126.1.

Dunning, D.J., Ross, Q., and Gladden, J. 1982. Evaluation of minimum size limits for St. Lawrence River northern pike. N. Am. J. Fish. Manag. **2**(2): 171–175. doi:10.1577/1548-8659(1982)2<171:EOMSLF>2.0.CO;2.

Edwards, F.E. 1991. A critique of three "economics" arguments commonly used to influence fishery allocations. N. Am. J. Fish. Manag. **11**(2): 121–130. doi:10.1577/1548-8675(1991)011<0121:ACOTEA>2.3.CO;2.

Fedler, A.J., and Ditton, R.B. 1994. Understanding angler motivations in fisheries management. Fisheries, **19**(4): 6–13. doi:10.1577/1548-8446(1994)019<0006:UAMIFM>2.0.CO;2.

Fisher, M.R. 1997. Segmentation of the angler population by catch preference, participation, and experience: a management-oriented application of recreation specialization. N. Am. J. Fish. Manag. **17**(1): 1–10. doi:10.1577/1548-8675(1997)017<0001:SOTAPB>2.3.CO;2.

Frost, W.E., and Kipling, C. 1967. A study of reproduction, early life, weight–length relationship and growth of pike, *Esox lucius* L., in Windermere. J. Anim. Ecol. **36**(3): 651–693. doi:10.2307/2820.

Gillis, K.S., and Ditton, R.B. 2002. A conjoint analysis of U.S.

Atlantic billfish fishery management alternatives. N. Am. J. Fish. Manag. **22**(4): 1218–1228. doi:10.1577/1548-8675(2002)022<1218:ACAOUS>2.0.CO;2.

Goeman, T.J., Spencer, P.D., and Pierce, R.B. 1993. Effectiveness of liberalized bag limits as management tools for altering northern pike population size structure. N. Am. J. Fish. Manag. **13**(3): 621–624. doi:10.1577/1548-8675(1993)013<0621:EOLBLA>2.3.CO;2.

Goodyear, C.P. 1993. Spawning stock biomass per recruit in fisheries management: foundation and current use. *In* Risk evaluation and biological reference points for fisheries management. *Edited by* S.J. Smith, J.J. Hunt, and D. Rivard. Can. Spec. Publ. Fish. Aquat. Sci. No. 120. pp. 67–81.

Hahn, J. 1991. Angler specialization: measurement of a key sociological concept and implications for fisheries management decisions. Am. Fish. Soc. Symp. **12**: 380–389.

Hanemann, W.M. 1984. Welfare evaluations in contingent valuation experiments with discrete responses. Am. J. Agric. Econ. **66**(3): 332–341. doi:10.2307/1240800.

Hilborn, R. 2007. Defining success in fisheries and conflicts in objectives. Mar. Policy, **31**(2): 153–158. doi:10.1016/j.marpol.2006.05.014.

Hubenova, T., Zaikov, A., and Vasileva, P. 2007. Investigation on fecundity, follicles and free embryo size of pond-reared pike (*Esox lucius*) of different age and size. Aquacult. Int. **15**(3–4): 235–240. doi:10.1007/s10499-007-9077-2.

Hunt, L. 2005. Recreational fishing site choice models: insights and future opportunities. Hum. Dimens. Wildl. **10**(3): 153–172. doi:10.1080/10871200591003409.

Jacobson, P.C. 1996. Trophy and consumptive value-per-recruit analysis for a walleye fishery. N. Am. J. Fish. Manag. **16**(1): 75–80. doi:10.1577/1548-8675(1996)016<0075:TACVPR>2.3.CO;2.

Johnson, B.M., and Carpenter, S.R. 1994. Functional and numerical responses: a framework for fish–angler interactions? Ecol. Appl. **4**(4): 808–821. doi:10.2307/1942010.

Kempinger, J.J., and Carline, R.F. 1978. Dynamics of the northern pike population and changes that occurred with a minimum size limit in Escanaba Lake, Wisconsin. Am. Fish. Soc. Spec. Publ. 11. American Fisheries Society, Bethesda, Md. pp. 382–389.

Kipling, C. 1983*a*. Changes in the growth of pike (*Esox lucius*) in Windermere. J. Anim. Ecol. **52**(2): 647–657. doi:10.2307/4578.

Kipling, C. 1983*b*. Changes in the population of pike (*Esox lucius*) in Windermere from 1944 to 1981. J. Anim. Ecol. **52**(3): 989–999. doi:10.2307/4469.

Kipling, C., and Frost, W.E. 1970. A study of mortality, population numbers, year class strengths, production and food consumption of pike, *Esox lucius* L., in Windermere from 1944 to 1962. J. Anim. Ecol. **39**(1): 115–157. doi:10.2307/2892.

Larkin, P.A. 1977. An epitaph for the concept of maximum sustainable yield. Trans. Am. Fish. Soc. **106**(1): 1–11. doi:10.1577/1548-8659(1977)106<1:AEFTCO>2.0.CO;2.

Le Cren, E.D., Kipling, C., and McCormack, J.C. 1977. A study of the numbers, biomass and year-class strengths of perch (*Perca fluviatilis* L.) in Windermere from 1941 to 1966. J. Anim. Ecol. **46**(1): 281–307. doi:10.2307/3961.

Lester, N.P., Marshall, T.R., Armstrong, K., Dunlop, W.I., and Ritchie, B. 2003. A broad scale approach to management of Ontario's recreational fisheries. N. Am. J. Fish. Manag. **23**(4): 1312–1328. doi:10.1577/M01-230AM.

Lester, N.P., Shuter, B.J., and Abrams, P.A. 2004. Interpreting the von Bertalanffy model of somatic growth in fishes: the cost of reproduction. Proc. R. Soc. Lond. Ser. B Biol. Sci. **271**(1548): 1625–1631. doi:10.1098/rspb.2004.2778.

Lewin, W.C., Arlinghaus, R., and Mehner, T. 2006. Documented and potential biological impacts of recreational fishing: insights for management and conservation. Rev. Fish. Sci. **14**(4): 305–367. doi:10.1080/10641260600886455.

Loomis, D.K., and Ditton, R.B. 1993. Distributive justice in fisheries management. Fisheries, **18**(2): 14–18. doi:10.1577/1548-8446(1993)018<0014:DJIFM>2.0.CO;2.

Lorenzen, K. 2008. Fish population regulation beyond stock and recruitment: the role of density-dependent growth in the recruited stock. Bull. Mar. Sci. **83**(1): 181–196.

Lorenzen, K., and Enberg, K. 2002. Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. Proc. R. Soc. Lond. Ser. B Biol. Sci. **269**(1486): 49–54. doi:10.1098/rspb.2001.1853.

Malvestuto, S.P., and Hudgins, M.D. 1996. Optimum yield for recreational fisheries management. Fisheries, **21**(6): 6–17. doi:10.1577/1548-8446(1996)021<0006:OYFRFM>2.0.CO;2.

Manski, C.F. 1977. The structure of random utility models. Theory Decis. **8**(3): 229–254. doi:10.1007/BF00133443.

Martinson, K.S., and Shelby, B. 1992. Encounter and proximity norms for salmon anglers in California and New Zealand. N. Am. J. Fish. Manag. **12**(3): 559–567. doi:10.1577/1548-8675(1992)012<0559:EAPNFS>2.3.CO;2.

Massey, D.M., Newbold, S.C., and Gentner, B. 2006. Valuing water quality changes using a bioeconomic model of a coastal recreational fishery. J. Environ. Econ. Manag. **52**(1): 482–500. doi:10.1016/j.jeem.2006.02.001.

Matlock, G.C., Saul, G.E., and Bryan, C.E. 1988. Importance of fish consumption to sport fishermen. Fisheries, **13**(1): 25–26. doi:10.1577/1548-8446(1988)013<0025:IOFCTS>2.0.CO;2.

McConnell, K.E., and Sutinen, J.G. 1979. Bioeconomic models of marine recreational fishing. J. Environ. Econ. Manag. **6**(2): 127–139. doi:10.1016/0095-0696(79)90025-1.

McFadden, D. 1974. Conditional logit analysis of quantitative choice behavior. *In* Frontiers in econometrics. *Edited by* P. Zarembka. Academic Press Inc., New York. pp. 105–142.

Oh, C.-O., and Ditton, R.B. 2006. Using recreation specialization to understand multi-attribute management preferences. Leis. Sci. **28**(4): 369–384. doi:10.1080/01490400600745886.

Oh, C.-O., Ditton, R.B., Anderson, D.K., Scott, D., and Stoll, J.R. 2005*a*. Understanding differences in nonmarket valuation by angler specialization level. Leisure Sci. **27**(3): 263–277. doi:10.1080/01490400590930899.

Oh, C.-O., Ditton, R.B., Gentner, B., and Riechers, R. 2005*b*. A stated preference choice approach to understanding angler preferences for management options. Hum. Dimens. Wildl. **10**(3): 173–186. doi:10.1080/10871200591003427.

Parkinson, E.A., Post, J.R., and Cox, S.P. 2004. Linking the dynamics of harvest effort to recruitment dynamics in a multistock, spatially structured fishery. Can. J. Fish. Aquat. Sci. **61**(9): 1658–1670. doi:10.1139/f04-101.

Paukert, C.P., Klammer, J.A., Pierce, R.B., and Simonson, T.D. 2001. An overview of northern pike regulations in North America. Fisheries, **26**(6): 6–13. doi:10.1577/1548-8446(2001)026<0006:AOONPR>2.0.CO;2.

Paulrud, A., and Laitila, T. 2004. Valuation of management policies for sport-fishing on Sweden's Kaitum River. J. Environ. Plann. Manag. **47**(6): 863–879. doi:10.1080/0964056042000284875.

Perman, R., Ma, Y., McGilvray, J., and Common, M. 2003. Natural resource and environmental economics. Pearson Education Limited, Harlow, Essex, U.K.

Peterson, J.T., and Evans, J.W. 2003. Quantitative decision analysis for sport fisheries management. Fisheries, **28**(1): 10–21. doi:10.1577/1548-8446(2003)28[10:QDAFSF]2.0.CO;2.

Pierce, R.B., and Tomcko, C.M. 1998. Angler noncompliance with slot length limits for northern pike in five small Minnesota lakes. N. Am. J. Fish. Manag. **18**(3): 720–724. doi:10.1577/1548-8675(1998)018<0720:ANWSLL>2.0.CO;2.

Pierce, R.B., and Tomcko, C.M. 2003. Interrelationships among production, density, growth, and mortality of northern pike in seven north-central Minnesota lakes. Trans. Am. Fish. Soc. **132**(1): 143–153. doi:10.1577/1548-8659(2003)132<0143:IAPDGA>2.0.CO;2.

Pierce, R.B., and Tomcko, C.M. 2005. Density and biomass of native northern pike populations in relation to basin-scale characteristics of north-central Minnesota lakes. Trans. Am. Fish. Soc. **134**(1): 231–241. doi:10.1577/T03-211.1.

Pierce, R.B., Tomcko, C.M., and Schupp, D.M. 1995. Exploitation of northern pike in seven small north-central Minnesota lakes. N. Am. J. Fish. Manag. **15**(3): 601–609. doi:10.1577/1548-8675(1995)015<0601:EONPIS>2.3.CO;2.

Pierce, R.B., Tomcko, C.M., and Margenau, T.L. 2003. Density dependence in growth and size structure of northern pike populations. N. Am. J. Fish. Manag. **23**(1): 331–339. doi:10.1577/1548-8675(2003)023<0331:DDIGAS>2.0.CO;2.

Post, J.R., Sullivan, M., Cox, S., Lester, N.P., Walters, C.J., Parkinson, E.A., Paul, A.J., Jackson, L., and Shuter, B.J. 2002. Canada's recreational fisheries: the invisible collapse? Fisheries, **27**(1): 6–17. doi:10.1577/1548-8446(2002)027<0006:CRF>2.0.CO;2.

Post, J.R., Mushens, C., Paul, A., and Sullivan, M. 2003. Assessment of alternative harvest regulations for sustaining recreational fisheries: model development and application to bull trout. N. Am. J. Fish. Manag. **23**(1): 22–34. doi:10.1577/1548-8675(2003)023<0022:AOAHRF>2.0.CO;2.

Post, J.R., Persson, L., Parkinson, E.A., and van Kooten, T. 2008. Angler numerical response across landscapes and the collapse of freshwater fisheries. Ecol. Appl. **18**(4): 1038–1049. doi:10.1890/07-0465.1. PMID:18536261.

Quinn, S.P. 1992. Angler perspectives on walleye management. N. Am. J. Fish. Manag. **12**(2): 367–378. doi:10.1577/1548-8675(1992)012<0367:APOWM>2.3.CO;2.

Radomski, P. 2003. Initial attempts to actively manage recreational fishery harvest in Minnesota. N. Am. J. Fish. Manag. **23**(4): 1329–1342. doi:10.1577/M01-231AM.

Radomski, P.J., and Goeman, T.J. 1996. Decision making and modeling in freshwater sport-fisheries management. Fisheries, **21**(12): 14–21. doi:10.1577/1548-8446(1996)021<0014:DMAMIF>2.0.CO;2.

Radomski, P.J., Grant, G.C., Jacobson, P.C., and Cook, M.F. 2001. Visions for recreational fishing regulations. Fisheries, **26**(5): 7–18. doi:10.1577/1548-8446(2001)026<0007:VFRFR>2.0.CO;2.

Rapp, T., Cooke, S.J., and Arlinghaus, R. 2008. Exploitation of specialised fisheries resources: the importance of hook size in recreational angling for large common carp (*Cyprinus carpio* L.). Fish. Res. **94**(1): 79–83. doi:10.1016/j.fishres.2008.06.019.

Roedel, P.M. (*Editor*). 1975. A summary and critique of the symposium on optimal sustainable yield. *In* Optimum sustainable yield as a concept in fisheries management. Am. Fish. Soc. Spec. Publ. 9. American Fisheries Society, Bethesda, Md. pp. 79–89.

Roth, B.M., Kaplan, I.C., Sass, G.G., Johnson, P.T., Marburg, A.E., Yannarell, A.C., Havlicek, T.D., Willis, T.V., Turner, M.G., and Carpenter, S.R. 2007. Linking terrestrial and aquatic ecosystems: the role of woody habitat in lake food webs. Ecol. Model. **203**(3–4): 439–452. doi:10.1016/j.ecolmodel.2006.12.005.

Schuhmann, P.W., and Schwabe, K.A. 2004. An analysis of congestion measures and heterogeneous angler preferences in a random utility model of recreational fishing. Environ. Resour. Econ. **27**(4): 429–450. doi:10.1023/B:EARE.0000018517.33432.0b.

Sullivan, M.G. 2002. Illegal angling harvest of walleyes protected by length limits in Alberta. N. Am. J. Fish. Manag. **22**(3): 1053–1063. doi:10.1577/1548-8675(2002)022<1053:IAHOWP>2.0.CO;2.

Sullivan, M.G. 2003. Active management of walleye fisheries in Alberta: dilemmas of managing recovering fisheries. N. Am. J. Fish. Manag. **23**(4): 1343–1358. doi:10.1577/M01-232AM.

Treasurer, J.W., Owen, R., and Bowers, E. 1992. The population dynamics of pike, *Esox lucius*, and perch, *Perca fluviatilis*, in a simple predator–prey system. Environ. Biol. Fishes, **34**(1): 65–78. doi:10.1007/BF00004785.

van Poorten, B.T., and Post, J.R. 2005. Seasonal fishery dynamics of a previously unexploited rainbow trout population with contrasts to established fisheries. N. Am. J. Fish. Manag. **25**(1): 329–345. doi:10.1577/M03-225.1.

Walker, J.R., Foote, L., and Sullivan, M.G. 2007. Effectiveness of enforcement to deter illegal angling harvest of northern pike in Alberta. N. Am. J. Fish. Manag. **27**(4): 1369–1377. doi:10.1577/M06-011.1.

Wallmo, K., and Gentner, B. 2008. Catch-and-release fishing: a comparison of intended and actual behavior of marine anglers. N. Am. J. Fish. Manag. **28**(5): 1459–1471. doi:10.1577/M07-062.1.

Willis, D.W. 1989. Proposed standard length–weight equation for northern pike. N. Am. J. Fish. Manag. **9**(2): 203–208. doi:10.1577/1548-8675(1989)009<0203:PSLWEF>2.3.CO;2.

Woodward, R.T., and Griffin, W.L. 2003. Size and bag limits in recreational fisheries: theoretical and empirical analysis. Mar. Resour. Econ. **18**(5): 239–262.

Worm, B., Hilborn, R., Baum, J.K., Branch, T.A., Collie, J.S., Costello, C., Fogarty, M.J., Fulton, E.A., Hutchings, J.A., Jennings, S., Jensen, O.P., Lotze, H.K., Mace, P.M., McClanahan, T.R., Minto, C., Palumbi, S.R., Parma, A.M., Ricard, D., Rosenberg, A.A., Watson, R., and Zeller, D. 2009. Rebuilding global fisheries. Science, **325**(5940): 578–585. doi:10.1126/science.1173146. PMID:19644114.

Appendix A. Sensitivity of predicted optimal regulations to fishery attributes

Table A1 appears on the following page.

Table A1. Sensitivity of predicted optimal regulations, and of the conditions that occur under these regulations, to the removal of single fishery attributes from the multi-attribute utility function (Table 1, eq. 1*b*).

	Angler population				
Removed attribute	Generic	Consumptive	Trophy	Average	Mixed (TU)
Optimal minimum-size limit (cm)					
Minimum-size limit	104 (+30.0%)	103 (+94.3%)	104 (+5.1%)	105 (+52.2%)	99 (+6.5%)
Crowding	60 (–25.0%)	51 (–3.8%)	96 (–3.0%)	50 (–27.5%)	99 (+6.5%)
Catch	51 (–36.3%)	23 (–56.6%)	100 (+1.0%)	52 (–24.6%)	93 (0.0%)
Average size	55 (–31.3%)	53 (0.0%)	101 (+2.0%)	61 (–11.6%)	61 (–34.3%)
Maximum size	62 (–22.5%)	52 (–1.9%)	86 (+13.1%)	69 (0.0%)	69 (–25.8%)
Optimal angler-license number					
Minimum-size limit	49 (–5.8%)	50 (+38.9%)	41 (+5.1%)	45 (+2.3%)	53 (–19.7%)
Crowding	20 (–61.5%)	31 (–13.9%)	88 (+125.6%)	12 (–72.7%)	100 (+51.5%)
Catch	56 (+7.7%)	40 (+11.1%)	42 (+7.7%)	47 (+6.8%)	75 (+13.6%)
Average size	55 (+5.8%)	44 (+22.2%)	42 (+7.7%)	48 (+9.1%)	46 (–30.3%)
Maximum size	51 (–1.9%)	39 (+8.3%)	44 (+12.8%)	44 (0.0%)	50 (–24.2%)
Annual realized angling effort under optimal regulations ($h \cdot ha^{-1}$)					
Minimum-size limit	61 (0.0%)	67 (+55.8%)	60 (+3.4%)	61 (+22.0%)	68 (+4.6%)
Crowding	19 (–68.9%)	33 (–23.3%)	114 (+96.6%)	13 (–74.0%)	70 (+7.7%)
Catch	63 (+3.3%)	44 (+2.3%)	59 (+1.7%)	49 (–2.0%)	64 (–1.5%)
Average size	64 (+4.9%)	55 (+27.9%)	59 (+1.7%)	53 (+6.0%)	57 (–12.3%)
Maximum size	58 (–4.9%)	46 (+7.0%)	61 (+5.2%)	49 (–2.0%)	59 (–9.2%)
Composition of anglers fishing in the mixed angling population under optimal regulations					
Minimum-size limit	0.35 (–14.6%)	0.31 (+121.1%)	0.34 (–24.9%)	na	na
Crowding	0.31 (–23.8%)	0.09 (–38.7%)	0.60 (+34.1%)	na	na
Catch	0.45 (+8.6%)	0.06 (–55.6%)	0.49 (+9.7%)	na	na
Average size	0.38 (–7.2%)	0.30 (+111.2%)	0.32 (–28.6%)	na	na
Maximum size	0.38 (–7.9%)	0.27 (+91.6%)	0.35 (–21.8%)	na	na
Spawning-potential ratio under optimal regulations					
Minimum-size limit	0.83 (+11.7%)	0.68 (+77.0%)	0.73 (–0.6%)	0.76 (+25.7%)	0.72 (–1.2%)
Crowding	0.76 (+2.2%)	0.42 (+10.0%)	0.56 (–23.1%)	0.66 (+9.3%)	0.71 (–2.3%)
Catch	0.42 (–43.8%)	0.13 (–65.6%)	0.72 (–0.7%)	0.38 (–37.3%)	0.74 (+0.8%)
Average size	0.43 (–41.8%)	0.34 (–12.5%)	0.72 (–0.9%)	0.49 (–18.5%)	0.48 (–34.7%)
Maximum size	0.56 (–24.5%)	0.37 (–3.9%)	0.68 (–7.2%)	0.61 (+0.2%)	0.57 (–22.3%)

Note: Results shown are for the multi-attribute scenario assuming total utility as the maximized social-welfare measure. Changes relative to results for the multi-attribute scenario with all fishery attributes included are given in parentheses. na, not applicable.

ERRATUM / ERRATUM

Erratum: Diversity and complexity of angler behaviour drive socially optimal input and output regulations in a bioeconomic recreational-fisheries model

Fiona D. Johnston, Robert Arlinghaus, and Ulf Dieckmann

Ref.: Can. J. Fish. Aquat. Sci. **67**: 1507–1531 (2010).

In Table 1 in the printed and online versions of the article, there are typesetting errors in eqs. 2*a*, 2*c*, and 7*e*. The correct versions are as follows:

[2*a*] $p_{fj} = \exp(\widehat{U}_{fj})/[\exp(U_n) + \exp(\widehat{U}_{fj})]$
[2*c*] $D_j = p_{Fj} D_{max}$
[7*e*] $C_{Hjt} = \min(C_{jt}, c_{max\,j} e_{jt}/\Psi)$.

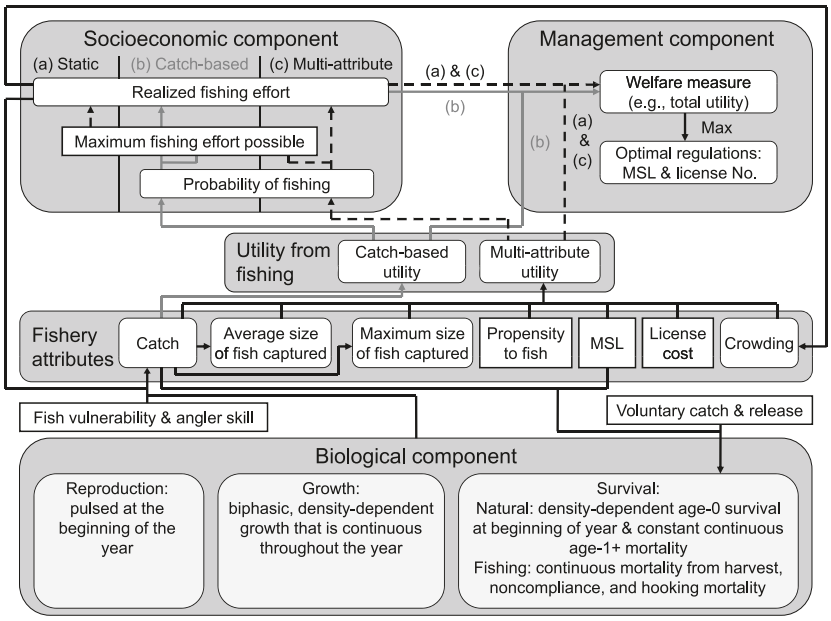
Figure 1 in the printed version of the article contains production errors. The correct version appears on the following page.

Received 7 September 2010. Accepted 7 September 2010. Published on the NRC Research Press Web site at cjfas.nrc.ca on 3 November 2010.
J22002

F.D. Johnston.[1] Evolution and Ecology Program, International Institute for Applied Systems Analysis, Schlossplatz 1, A-2361 Laxenburg, Austria; Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany; Inland Fisheries Management Laboratory, Department for Crop and Animal Sciences, Faculty of Agriculture and Horticulture, Humboldt-University of Berlin, Philippstrasse 13, Haus 7, 10115 Berlin, Germany.
R. Arlinghaus. Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany; Inland Fisheries Management Laboratory, Department for Crop and Animal Sciences, Faculty of Agriculture and Horticulture, Humboldt-University of Berlin, Philippstrasse 13, Haus 7, 10115 Berlin, Germany.
U. Dieckmann. Evolution and Ecology Program, International Institute for Applied Systems Analysis, Schlossplatz 1, A-2361 Laxenburg, Austria.

[1]Corresponding author (e-mail: johnston@iiasa.ac.at).

Fig. 1. Simplified flow diagram illustrating interactions among the three model components of our bioeconomic modelling approach: the biological component, the socioeconomic component, and the management component. The model included three angler-behaviour scenarios: (*a*) static angler behaviour, where anglers fished at the maximal rate, (*b*) catch-based dynamic angler behaviour, where anglers responded to the fishery based on catch rates, and (*c*) multi-attribute dynamic angler behaviour, where anglers responded to the fishery based on a multi-attribute utility function. Black solid arrows depict influences that apply across all scenarios, while gray arrows apply to the catch-based scenario only and black broken arrows apply to either the static or multi-attribute scenario, as is also indicated by labels beside the arrows. Factors in round-cornered boxes dynamically changed throughout model runs, while parameters for factors in square-cornered boxes were held constant.



Paper III

III

Johnston, F. D., R. Arlinghaus, and U. Dieckmann. 2013. Fish life history, angler behaviour and optimal management of recreational fisheries. Fish and Fisheries 14(4): 554-579.

FISH and FISHERIES

FISH and FISHERIES, 2013, **14**, 554–579

Fish life history, angler behaviour and optimal management of recreational fisheries

Fiona D Johnston[1,2,3], *Robert Arlinghaus*[1,3] *& Ulf Dieckmann*[2]

[1]Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587, Berlin, Germany, [2]Evolution and Ecology Program, International Institute for Applied Systems Analysis, Schlossplatz 1, A-2361, Laxenburg, Austria and [3]Inland Fisheries Management Laboratory, Department for Crop and Animal Sciences, Faculty of Agriculture and Horticulture, Humboldt-University of Berlin, Philippstrasse 13, Haus 7, 10115, Berlin, Germany

Abstract

To predict recreational-fishing impacts on freshwater fish species, it is important to understand the interplay between fish populations, anglers and management actions. We use an integrated bioeconomic model to study the importance of fish life-history type (LHT) for determining (i) vulnerability to over-exploitation by diverse angler types (generic, consumptive and trophy anglers), who respond dynamically to fishing-quality changes; (ii) regulations [i.e., minimum-size limits (*MSLs*) and licence densities] that maximize the social welfare of angler populations; and (iii) biological and social conditions resulting under such socially optimal regulations. We examine five prototypical freshwater species: European perch (*Perca fluviatilis*), brown trout (*Salmo trutta*), pikeperch (*Sander lucioperca*), pike (*Esox lucius*) and bull trout (*Salvelinus confluentus*). We find that LHT is important for determining the vulnerability of fish populations to overfishing, with pike, pikeperch, and bull trout being more vulnerable than perch and brown trout. Angler type influences the magnitude of fishing impacts, because of differences in fishing practices and angler-type-specific effects of LHT on angling effort. Our results indicate that angler types are systematically attracted to particular LHTs. Socially optimal minimum-size limits generally increase with LHT vulnerability, whereas optimal licence densities are similar across LHTs. Yet, both regulations vary among angler types. Despite this variation, we find that biological sustainability occurs under socially optimal regulations, with one exception. Our results highlight the importance of jointly considering fish diversity, angler diversity and regulations when predicting sustainable management strategies for recreational fisheries. Failure to do so could result in socially suboptimal management and/or fishery collapse.

Keywords Angler-effort dynamics, bioeconomic model, density-dependent compensation, life history, optimal management, utility

Correspondence:
Fiona D Johnston, Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany
Tel.: +49-(0)30-64181-653
Fax: +49-(0)30-64181-750
E-mail: johnston@igb-berlin.de

Received 29 Jan 2011
Accepted 22 May 2012

 DOI: 10.1111/j.1467-2979.2012.00487.x

Introduction

Commercial harvesting can cause severe declines in fish stocks (Worm *et al.* 2009). Similarly, recreational fisheries can also have substantial negative impacts on the world's fisheries (McPhee *et al.* 2002; Coleman *et al.* 2004; Cooke and Cowx 2004; Lewin *et al.* 2006), although they often remain 'invisible' because of absent or insufficient monitoring (Post *et al.* 2002). The lack of sustainability in some fisheries may relate to simplification or neglect of three interrelated factors, which need to be jointly considered in fisheries management: (i) the life history of the exploited population and its influence on vulnerability to over-exploitation (Reynolds *et al.* 2001; Rose *et al.* 2001; Winemiller 2005), (ii) the heterogeneity and dynamics of fishers exploiting the fishery (Radomski *et al.* 2001; Wilen *et al.* 2002; Johnston *et al.* 2010; Fulton *et al.* 2011) and (iii) the influence of management objectives and regulations on the ecological and social dynamics of the fishery (Radomski *et al.* 2001; Cox and Walters 2002; Wilen *et al.* 2002). Only by integrating these three main components – biological, social and managerial – into fisheries-projection models (Fig. 1) can fisheries dynamics be understood and more robust management predictions be achieved (Johnston *et al.* 2010). While earlier studies have illustrated the importance of considering how differences in fish biology (e.g., productivity) can influence the efficacy of harvest regulations (e.g., Beamesderfer and North 1995), progress in integrated angler-fish population modelling has been slow (Fenichel *et al.* 2012). To our knowledge, no previous modelling study has rigorously explored the importance of considering the interrelationships between fish life history, angler diversity and various management measures for sustainable fisheries management. To advance our understanding, here we examine these interrelationships and study how the resulting dynamics of both fish and anglers affect optimal management strategies in recreational fisheries.

A key factor determining the dynamics of a fishery is fish life history (described by the combination of life-history traits that characterize a species), because it influences a fish population's vulnerability to over-exploitation (Reynolds *et al.* 2001; Rose *et al.* 2001; Winemiller 2005). Life-history traits (describing, e.g., growth, maturation or fecundity) vary substantially among species (Reynolds *et al.* 2001) and are often phenotypically plastic (Pigliucci 2005). Fish that exhibit different life-history strategies will differ in their

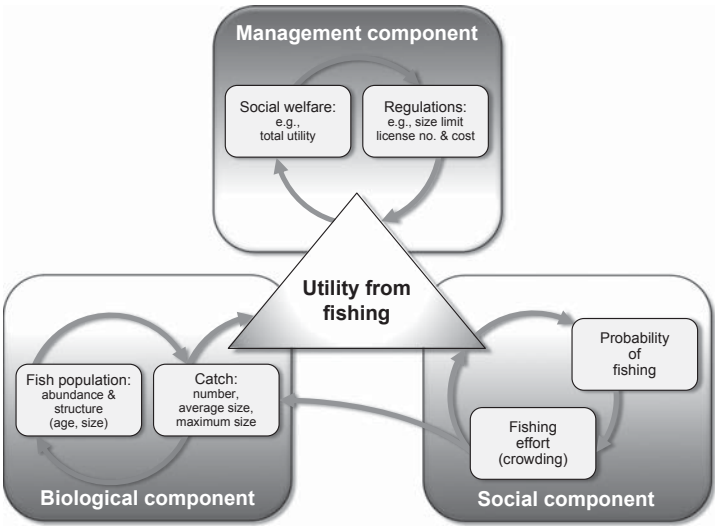


Figure 1 Fishery components and their interactions. For an overview of the corresponding integrated bioeconomic model, see Fig. 2.

production and in the degree to which density-dependent processes regulate the population, thus altering their ability to compensate for fishing mortality (Rose *et al.* 2001; Winemiller 2005; Goodwin *et al.* 2006). For example, fish that mature late, attain large maximum size and have low potential rates of population increase have been reported to be more vulnerable to over-exploitation than fish with the opposite characteristics (Jennings *et al.* 1998). However, for freshwater fish species, the relationships between risk of decline and anthropogenic factors are often not clear-cut (Duncan and Lockwood 2001; Reynolds *et al.* 2005). Thus, to provide more robust predictions about the vulnerability of freshwater fish populations to over-exploitation by recreational angling, a quantitative modelling approach that describes life-history characteristics of commonly targeted species is warranted.

A second key, yet often ignored, factor determining the impacts of fishing on fish populations is the structure and dynamics of fishers exploiting the fishery (Wilen *et al.* 2002; Johnston *et al.* 2010; Fulton *et al.* 2011). While commercial fishers are primarily motivated by maximizing yield or economic revenue (Hilborn 2007), multiple catch-related and non-catch-related attributes of a fishery (e.g., catch rates, fish size, angler congestion, aesthetic appeal, facilities, permit costs; reviewed in Hunt 2005) influence the fishing decisions of recreational anglers. Furthermore, angler populations are almost always composed of diverse angler types (e.g., Arlinghaus 2004), each exhibiting specific fishing preferences and fishing practices (e.g., Aas *et al.* 2000; Beardmore *et al.* 2011). For example, some anglers prioritize fish harvest, whereas others preferentially target trophy-sized fish and voluntarily release them (Hahn 1991; Jacobson 1996; Fisher 1997). Thus, angling impacts likely differ with the type of anglers fishing (Johnston *et al.* 2010) and the life-history type (LHT) of exploited fish. Predicting the long-term outcome of fish–angler interactions requires an integrated modelling approach that incorporates population dynamics of diverse fish life histories and behavioural responses of diverse angler types to changes in fishery quality (Johnston *et al.* 2010).

A third key factor influencing any fishery system is its management component. Fish-angler dynamics do not occur in isolation from fishing regulations. Harvest regulations commonly employed in recreational fisheries influence which fish are caught and/or harvested (in terms of, e.g., species and size), but they also influence angler behaviour (Beard *et al.* 2003; Johnston *et al.* 2011) and therefore are of crucial importance for describing angler dynamics (Johnston *et al.* 2010). Fish–angler dynamics will influence how effective regulations are at meeting the management objectives they are designed to achieve, objectives that often include balancing the sometimes conflicting interests of different stakeholders with the maintenance of a biologically sustainable fishery (Cochrane 2000; Cox and Walters 2002; Hilborn 2007). Optimum social yield (OSY) incorporates numer-

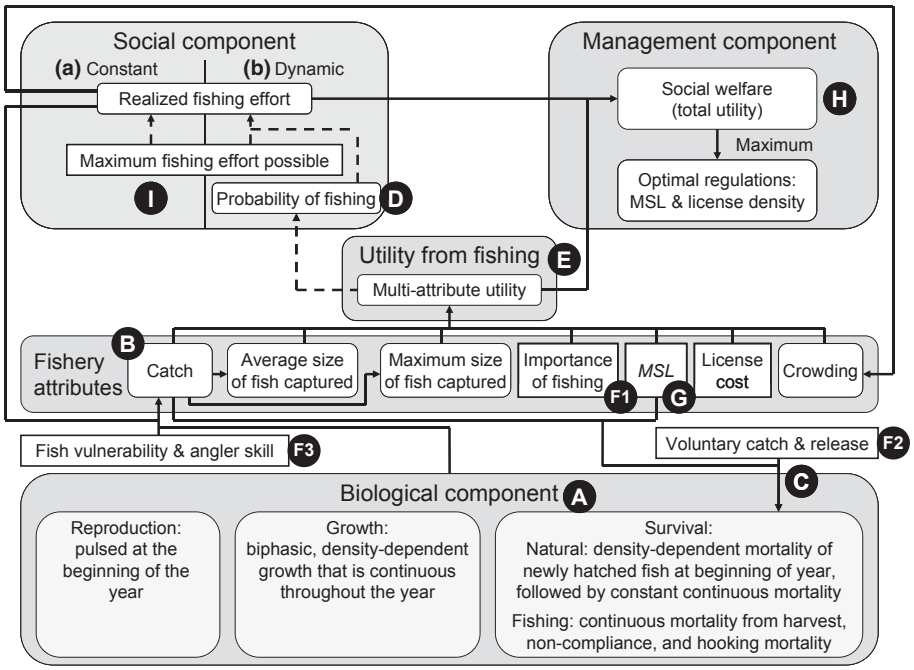


Figure 2 Schematic overview of the integrated bioeconomic model. Alphabetized black circles indicate model elements described in the section 'Methods, Model components'. Dashed lines highlight differences between model scenarios with constant vs. dynamic fishing effort. *MSL*, minimum-size limit.

ous management objectives by integrating social, economic and biological considerations into a single measure of the utility (in terms of benefits, satisfaction and/or social welfare) a recreational fishery provides to society (Roedel 1975; Malvestuto and Hudgins 1996). The OSY approach is rarely used in practice (possibly because of the difficulty in measuring the underlying quantities), but has shown promise for the management of a northern-pike (*Esox lucius*, Esocidae) recreational fishery: a study modelling this species revealed that regulations maximizing social welfare also maintained a biologically sustainable fish population (Johnston *et al.* 2010). However, because life history influences a fish population's response to fishing, and in turn the behaviour of the anglers exploiting it, it is unknown if this prediction holds across life histories commonly targeted by freshwater recreational anglers.

To explore the importance of jointly considering fish life history, dynamic and diverse angler behaviour, alternative management options and the nonlinear interplay between the three fishery components (Fig. 1) when managing recreational fisheries, here we use an integrated bioeconomic model. Our model is parameterized to describe five fish LHTs representing recreationally important freshwater fish species, in conjunction with three plausible angler behavioural types (Johnston *et al.* 2010). We use this model to evaluate how differences in LHT and angler type influence recreational-fishing impacts and the socially optimal management of fisheries. Specifically, we investigate (i) how LHT influences vulnerability to overfishing under different levels of constant and, more realistically, dynamic fishing effort by various angler types; (ii) how angling regulations (e.g., minimum-size limits and licence densities) that maximized social welfare vary between LHTs and angler types; and finally (iii) how biological sustainability and social conditions under socially optimal regulations differ across LHTs and angler types. Our intention here is not to provide predictions for a particular fishery, but to gain general insights into the influence of LHT and angler diversity on the dynamics of a coupled social–ecological system, by bridging the traditional divide between fisheries science and social science (Arlinghaus *et al.* 2008; Fulton *et al.* 2011; Fenichel *et al.* 2012). Our framework can nevertheless be calibrated to a particular fishery, if appropriate data on the fish population and the preferences of

angler types are collected using fisheries-biological and human-dimensions research methods.

Methods

Model overview

We use an integrated bioeconomic model (Table A1), developed by Johnston *et al.* (2010) for a northern-pike recreational fishery, that links dynamic angler behaviour with a deterministic age-structured fish population model for a single-species, single-lake fishery. The model includes three components (Figs 1 and 2): (i) a biological component that determines the fish population dynamics of different LHTs, (ii) a social component that determines the angler-effort dynamics of different angler types based on angler-type-specific preference functions and (iii) a management component that prescribes the angling regulations. In this study, we extend the model by Johnston *et al.* (2010) to describe five distinct LHTs representing northern pike, European perch (*Perca fluviatilis*, Percidae), pikeperch (*Sander lucioperca*, Percidae), brown trout (*Salmo trutta*, Salmonidae) and bull trout (*Salvelinus confluentus*, Salmonidae) (Fig. 3; Table S1). These LHTs were chosen because they span diverse life-history characteristics (Wootton 1984) and represent a broad range of LHTs commonly targeted by freshwater recreational anglers (e.g., Post *et al.* 2002; Almodóvar and Nicola 2004; Isermann *et al.* 2007). The LHTs vary in body size and growth rate, age- and size-at-maturation, offspring size, fecundity, lifespan, natural mortality rate and the degree to which density regulates early juvenile survival (stock–recruitment relationships) and individual growth rates (Fig. 3). Thus, the LHTs examined here differ in unexploited abundance, biomass and age and size-structure (Table 1). To allow for a direct comparison of model outcomes, the same age-structured fish population model is used for all LHTs. In all scenarios we investigate, fish populations reach demographic equilibrium prior to the introduction of fishing, and the presented results reflect equilibrium conditions after fishing is introduced (i.e., we investigate long-term dynamics). A model overview is provided below (see also Fig. 2); additional details are described in the study by Johnston *et al.* (2010). Model equations are given in Table A1 and variables are given in Table A2, qualitative descriptions of LHTs and angler types are shown in Figs 3 and 4, and detailed parameters and part-worth-utility (PWT) equations are provided in the supplementary material (Tables S1–S4).

Model components

The biological model component determines fish population dynamics, describing reproduction, growth and survival (Fig. 2, element A). Reproduction is pulsed at the beginning of the year. To account for LHT differences in spawning time (not present in Johnston *et al.* 2010), fecundities (total egg numbers) are determined by spawner sizes and spawner numbers either at the beginning of each year (spring spawners) or in the fall of the previous year (fall spawners) (Table A1, Equation 5a; Table S1). Two important density-dependent processes, growth in body size and early offspring survival, allow for compensatory responses to exploitation (Rose *et al.* 2001; Lorenzen 2008). Density-dependent offspring survival from spawning to post-hatch occurs at the beginning of each year, described by either a Beverton–Holt type (Beverton and Holt 1957) or a Ricker-type stock–recruitment relationship (Ricker 1954b) (Table A1, Equation 5c). Growth is modelled using a biphasic growth model (Lester *et al.* 2004) (Table A1, Equation 4a–c). Growth, as well as mortality from both fishing and natural sources (for fish aged 1 year and older; Table A1, Equation 6i), is modelled in continuous time. Continuous growth allows fish to become more vulnerable to capture within a year. Continuous mortality allows for recapture and repeated exposure of released fish to hooking mortality; the latter can have serious negative impacts on some recreational fish species especially if effort is high (Coggins *et al.* 2007). The number and size of fish caught are determined jointly by the abundance and structure of the fish population, fishing effort, anglers' skills (affecting catchability) and the size-dependent vulnerability to capture (Table A1, Equation 6a), which varies among angler types (see below) (Table A1, Equation 6c; Fig. 2, element B). Fishing mortality depends on the number and size distribution of the catch, the regulated minimum-size limit and harvest practices of angler types fishing (Table A1, Equation 6h; Fig. 2, element C). Thus, fishing mortality is size dependent through both capture vulnerability and minimum-size limit.

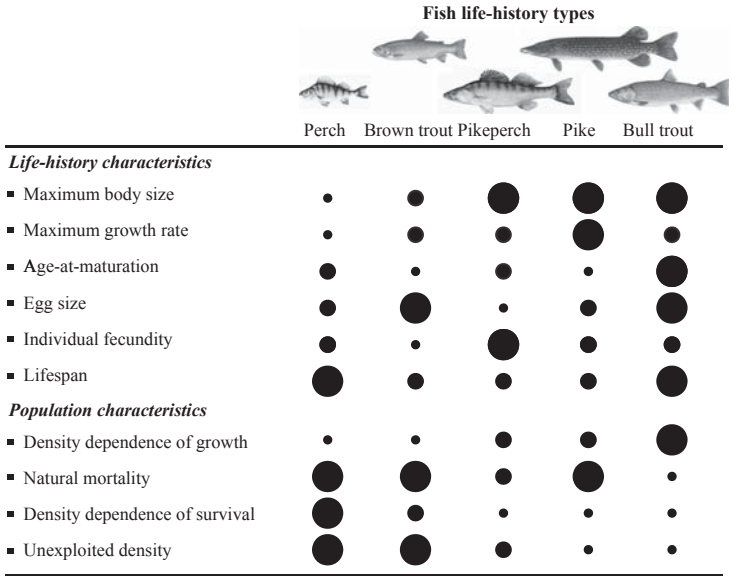


Figure 3 Qualitative description of variation in biological characteristics among the five considered fish life-history types. Small, medium and large circles represent low/small, intermediate and high/large levels, respectively. See Table S1 for parameters.

Table 1 Characteristics of fish life-history types under unexploited conditions.

	Life-history type				
	Perch	Brown trout	Pikeperch	Pike	Bull trout
Maximum body size (cm; L_{max}, Table S1)	38.5	51.5	103	117	98
Density of fish aged 1 year and older (ha^{-1})	779	300	97	23	12
Biomass fish aged 1 year and older (kg ha^{-1})	49.1	29.5	61.0	16.1	10.0
Maximum annual growth increment of juveniles (cm)	5.5	8.4	10.0	20.7	7.7
Proportion of adults in population	0.44	0.57	0.45	0.63	0.36
Proportion of first-time spawners in mature population	0.34	0.43	0.24	0.37	0.19
Mean age (years)	2.97	2.33	4.11	2.70	5.14
Age-at-maturation (years; a_m, Table S1)	3	2	4	2	6
Mean length (cm)	13.0	17.6	31.8	40.0	33.7
Size-at-maturation (cm)	14.8	18.4	36.1	35.3	45.7
Relative fecundity (g^{-1})	65.6	1.9	150.0	25.5	1.9
Maximum recruitment density of fish aged 0 (ha^{-1})*	601.2	160.8	24.6	9.2	2.5

*Either asymptotic value of Beverton–Holt stock–recruitment relationship or peak value of Ricker stock–recruitment relationship.

The social model component determines annual fishing effort. Random utility theory assumes that anglers will have a higher probability to fish when conditions provide them with more utility (Hunt 2005) (Fig. 2, element D). Following Johnston *et al.* (2010), angling effort is determined by angler-type-specific multi-attribute utility functions, based on catch-related attributes (catch rates, average and maximum size of fish caught) and non-catch-related attributes (angler crowding, minimum-size limit and licence cost) of the fishery that are known to affect anglers' utility and hence participation decisions (Hunt 2005) (Table A1, Equation 1; Fig. 2, element E). In addition, angler types can differ in their fishing practices (in terms of the size of fish they target, their skill level and their propensity to voluntarily release fish), as well as in their preferences for the considered fishery attributes (Aas *et al.* 2000; Hunt 2005; Oh and Ditton 2006). Here, we describe three angler types – generic, consumptive, and trophy anglers – differing in their fishing practices and preferences (Fig. 2, elements F1 to F3; see also Fig. 4). Our parameterization of utility functions for these three

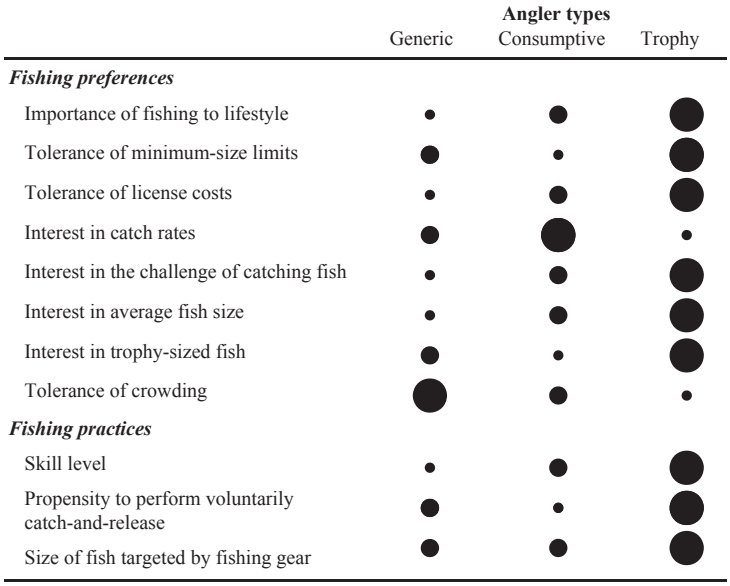


Figure 4 Qualitative description of angler-type diversity in preferences for fishery attributes and fishing practices. Small-, medium- and large-sized dots indicate low/small, intermediate and high/large levels, respectively.

angler types (Table S3) is based on angler specialization theory (Bryan 1977) as described in detail in the study by Johnston *et al.* (2010).

The management model component prescribes input regulations through licence densities (A_Ls) and output regulations through minimum-size limits (*MSL*s) (Fig. 2, element G). In our model, licence density is the number of licences issued to anglers for a single 100-ha lake, and ranges up to a maximum of one licence per hectare. We focus on *MSL*s, as these are commonly used in recreational fisheries to limit harvest (Radomski *et al.* 2001). In open-access recreational fisheries, output regulations often only reduce an individual angler's harvest, and not total harvest (Radomski *et al.* 2001; Cox and Walters 2002; Cox *et al.* 2002), whereas input regulations more directly control angler effort and thus fishing mortality (Cox *et al.* 2002); therefore, licence densities are also varied in our model. We do not include daily bag limits in our model for three reasons. First, we want to concentrate our analyses on comparing one input regulation and one output regulation. Second, the effectiveness of daily bag limits has been questioned, because in practice daily quotas are often not met (Cook *et al.* 2001) and moreover are only successful if fishing effort and thus total harvest are not too high (Post and Parkinson 2012). Third, our model includes angler-type-specific harvest preferences, which work similar to daily bag limits, by limiting some angler types' daily harvest through their propensity to voluntarily release fish (Table S3). The management component of our model is also used to determine regulations that achieve an OSY. We assume such optimal regulations to be given by combinations of minimum-size limit (MSL_{opt}) and licence density ($A_{L,opt}$) that maximize the total utility (an aggregation of individual utilities across anglers; Table A1, Equation 7b) gained by the angler population at equilibrium (Fig. 2, element H). We use total utility to measure social welfare; naturally, results may differ when other welfare measures are used (Johnston *et al.* 2010).

Standardizing across LHTs

To allow direct comparison among our results for different LHTs, the vulnerability of fish to capture, as well as some baseline attribute levels used for determining angler utility that depend on fish size or abundance, needs to be standardized for LHT differences in maximum body size (L_{max}) and unexploited abundance (Table 1).

Vulnerability to capture

The size dependence of capture vulnerability is described by a sigmoidal function that varies between LHTs and angler types. These functions are characterized by the size L_{50} at which vulnerability reaches 50%, and by the steepness y with which vulnerability increases around L_{50} (Table A1, Equation 6a). In choosing L_{50} and y, we need to account for three considerations. First,

to standardize the vulnerability curve among LHTs, we allow L_{50} to increase roughly proportionally with a LHT's maximum size L_{max}. Second, to produce realistic size-structures of catch, we need to account for a systematic bias in L_{50}: the general lack of interest in catching very small fish, presumably because they provide minimal consumptive or trophy value, reduces the relative range of sizes captured for smaller LHTs much more than it does for larger LHTs. Empirical findings show that even when anglers target smaller-bodied predatory freshwater species, they catch few very small fish (e.g., van Poorten and Post 2005; Wilberg *et al.* 2005). We account for this bias by introducing an offset L_{shift} into the sigmoidal function that shifts L_{50} to the right. Because it is independent of $L_{max,}$ this shift L_{shift} is more consequential for smaller LHTs than for larger LHTs and thus accounts for the aforementioned bias. Third, different angler types impose different size-selective capture vulnerabilities, with trophy anglers targeting larger fish. We account for these three considerations by determining L_{50} as a linear function of L_{max}, $L_{50} = z_j L_{max} + L_{shift}$ (Table A1, Equation 6b) where z_j depends on the angler type j. To estimate y and z_j for generic and consumptive anglers, we use a least-square approximation of the vulnerability of pike reported by Johnston *et al.* (2010). For trophy anglers, z_j is increased by 10% relative to generic and consumptive anglers (Table S3), because trophy anglers value, and thus target, larger fish by using different gear than the other angler types (Jacobson 1996; Aas *et al.* 2000). To the extent that empirical data are available, we find that the capture vulnerabilities thus specified produce size-structures of catch that generally match empirical observations for the described LHTs or closely related species (e.g., Paul *et al.* 2003; Post *et al.* 2003; van Poorten and Post 2005; Wilberg *et al.* 2005; Arlinghaus *et al.* 2009; see footnote Table S3).

Part-worth-utility functions

In our model, multiple fishery attributes contribute to an angler's utility (Table A1, Equation 1) and thus influence the participation decisions of anglers (Table A1, Equation 2a). PWU functions from welfare economics (illustrated in Johnston *et al.* 2010; Fig. 3) are used to describe the relative importance of each catch-related and non-catch-related attribute to an angler's overall utility (Table S2). The PWU functions also involve scaling attribute levels relative to baseline attribute levels (defined as the levels at which the focal PWU value equals 0, and the probability to fish thus equals 50%, when all other PWU values equal 0; Table S4). However, some baseline attribute levels depend on fish size or fish abundance in a way that varies with LHT. For example, a perch angler likely gains more utility from catching a 30-cm perch than a pike angler does from catching a 30-cm pike, because of the intrinsic size differences between these two species. Thus, several baseline attribute levels are standardized so as to achieve such the desired relative scaling across LHTs.

First, *MSLs* are set as a proportion of L_{max} ranging between 0 and 1 (Table S4). Second, the baseline catch rates C_{De} (Table S4) are assumed to equal 50% of the maximum catch rate achievable for a given LHT by a mixed angler population (comprising 40%, 30% and 30%; generic, consumptive and trophy anglers, respectively) imposing no harvest, non-compliance or hooking mortality on the fish population. For all LHT, the thus established baseline catch rates are generally within the range reported for the modelled, or closely related, species (see Table S4). Third, proportional-stock-density (PSD) categories (Gabelhouse 1984), also known as proportional size-structure (Guy *et al.* 2006), which describe the recreational value of fish based on their size relative to the species' world-record length, are used to set baseline values for the average size $\bar{L}_e$ and maximum size L_{xe} of caught fish. Specifically, we assume that 'quality' fish (40% of L_{max}) represent the baseline value for $\bar{L}_e$, and fish bordering the 'preferred' and 'memorable' categories (55% of L_{max}) represent the baseline value for L_{xe} (Table S4).

Outline of analysis

To examine how biological impacts from recreational fishing vary among LHTs, we first run our model across a range of *MSLs* (Table S1) and fishing efforts, both of which are held constant within a model run. In these model runs, anglers therefore do not behave dynamically (Fig. 2, element I) and are furthermore assumed to be consumptive anglers killing all harvestable fish: this makes it possible to compare the biological response of LHTs at equilibrium to identical levels of fishing effort. Changes in fish abundance and biomass relative to unexploited levels (Table 1), and in the

weighted spawning-potential ratio *SPR* (Table A1, Equation 7a), are examined. The *SPR* is commonly used to assess fisheries sustainability: values below 0.2–0.3 are considered critical (Goodyear 1993), whereas maintaining *SPR* above 0.35–0.40 is likely to prevent recruitment overfishing (Mace 1994; Clark 2002).

In a second stage of our analysis, we allow angler types to respond dynamically to the perceived quality of the fishery, that is, utility affected anglers' probability to fish (Fig. 2, element D). We examine model runs across a range of *MSL*s and licence densities A_L (Table A2), for homogeneous angler populations composed of one angler type and, more realistically, for four specific compositions of mixed angler populations (Table S3). These mixed angler populations comprise either relatively equal proportions of the three angler types (40:30:30%; generic, consumptive and trophy anglers, respectively) or strongly skewed towards generic (70%:15%:15%), consumptive (15%:70%:15%) or trophy (15%:15%:70%) anglers. We evaluate how the interplay between life histories, dynamic angler behaviours and regulations differentially affects overfishing vulnerability, angler behaviour and optimal regulations (in terms of MSL_{opt} and $A_{L,opt}$) across LHTs and anglers populations under equilibrium conditions. The biological conditions (in terms of *SPR*) and social conditions (in terms of total utility and fishing effort) under optimal regulations are also examined, to assess whether trends across LHTs exist and whether optimal regulations imply biological sustainability. We also analyse the relative participation of angler types in mixed angler populations (in terms of the proportion of the fishing effort exerted by a given angler type relative to that type's proportion of the angler population; Table A1, Equation 7c) across LHTs, to determine whether angler types are differentially attracted to, or excluded from, particular fisheries.

Finally, we evaluate the sensitivity of fish-angler dynamics to LHT parameterization using elasticity analyses (e.g., Allen *et al.* 2009). For this purpose, we vary each life-history parameter by ±10% from its original value (except for age-at-maturation and maximum age, which are discrete and are therefore varied by ±1 year) and calculate the relative change in MSL_{opt} and $A_{L,opt}$. Relative changes exceeding 10% indicate that the fish-angler dynamics are sensitive to those parameters. *SPR* levels predicted under the new optimal regulations are also examined, to evaluate whether predictions about biological sustainability under socially optimal regulations are robust to changes in life-history parameters.

Results

Biological impacts under constant fishing effort

In the absence of exploitation, the five LHTs in our model differ substantially in their population characteristics. Perch is most abundant, with an unexploited equilibrium density (of fish aged 1 year and older) approaching 800 fish ha^{-1}, followed by brown trout and pikeperch (300 and 90 fish ha^{-1}, respectively; Table 1). Pike and bull trout are least abundant (<25 fish ha^{-1}; Table 1). Predicted abundance under unexploited conditions generally fall within the range predicted in the literature, although pikeperch in our model are more abundant than what may be considered average literature values, and the predicted abundances of perch and bull trout are at the low end of the range reported in the literature (Data S1). The unexploited biomasses (of fish aged 1 year and older) predicted by our model range between 10 and 60 kg ha^{-1} across all LHTs. Pikeperch exhibits the highest unexploited biomass, followed by perch, brown trout, pike and bull trout.

When recreational fishing is introduced with a constant consumptive angling effort, the biological impacts on the five LHTs, measured relative to unexploited conditions, differ greatly (Fig. 5). Fishing reduces the abundance, biomass and *SPR* of pike, bull trout and pikeperch relative to unexploited levels, particularly under low to moderately restrictive *MSL*s (0–50% of L_{max}) and moderate to high fishing efforts (30–80 h ha^{-1}; Fig. 5). Similarly, fishing reduces the biomass and *SPR* of perch and brown trout (Fig. 5), although their relative magnitudes of decline are generally smaller than for the other LHTs. However, unlike all other LHTs, exploitation increases perch abundance above unexploited levels under all examined *MSL*s and fishing efforts (Fig. 5). Fishing also increases brown-trout abundance (Fig. 5), but only under liberal *MSL*s and for fishing efforts below 20 h ha^{-1}, or under more restrictive *MSL*s above 60% of L_{max}.

Overall, these results suggest that the susceptibility of LHTs to declines in abundance, biomass and *SPR* is greatest to least as follows (ranked by the proportion of model runs in which *SPR* was

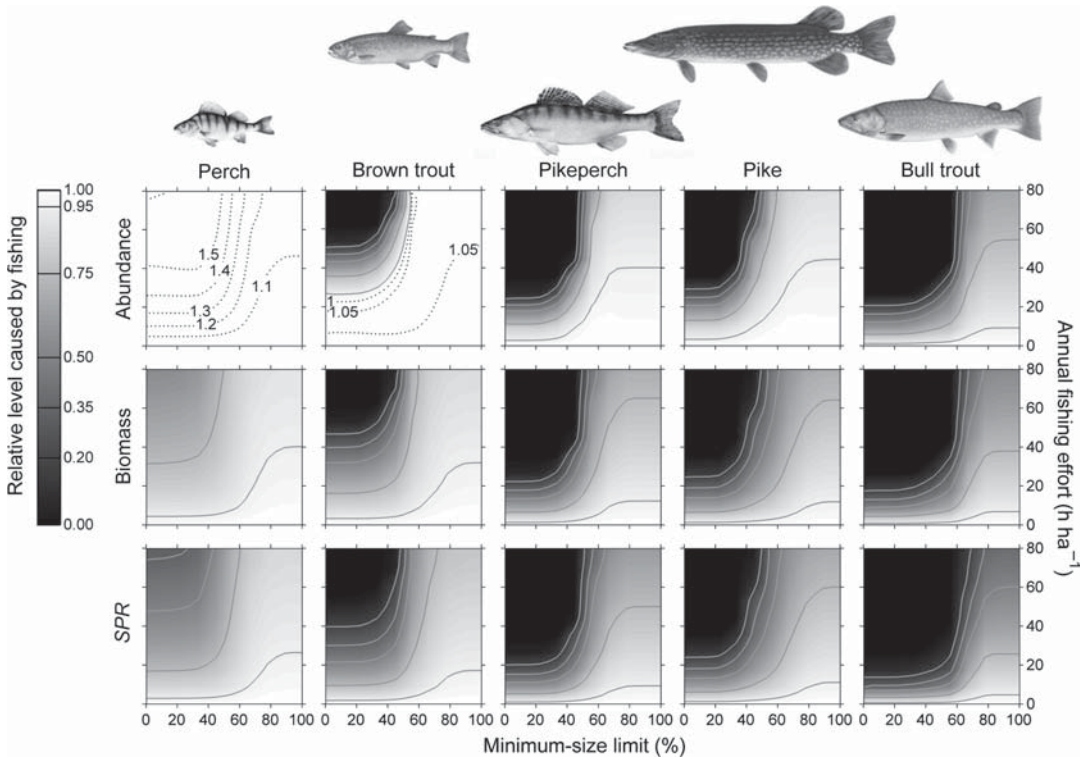


Figure 5 Impacts of fishing, over a range of minimum-size limits (as a percentage of L_{max}) and annual fishing efforts, on the density of aged 1 year and older, on the biomass of fish aged 1 year and older and on the spawning-potential ratio *SPR* (rows), across the five considered fish life-history types (columns). The shown levels correspond to fished conditions relative to unexploited conditions. Continuous contours represent relative levels smaller than 1 (greyscale bar). Dotted contours represent values relative levels >1. All panels are based on considering consumptive anglers fishing with constant effort and harvesting all harvestable fish caught.

smaller than 0.35): bull trout, pikeperch/pike (similar responses), brown trout and perch. Hereafter, we use the term 'LHT vulnerability' to refer the degree to which LHTs in our model are susceptible to recruitment overfishing from recreational angling. The obtained ranking suggests that LHT vulnerability to over-exploitation by consumptive anglers is negatively related to unexploited abundance and maximum recruitment, positively related to maximum body size and size-at-maturation and not strongly related to age-at-maturation, relative fecundity, or natural mortality (see Table 1 and Table S1 for values).

Biological impacts under dynamic angler behaviour

Allowing anglers to respond dynamically to the perceived quality of the fishery alters the incidence of recruitment overfishing and also causes fishing efforts to vary substantially between LHTs and angler populations (Fig. 6). Despite this influence of LHT on the angling effort a fishery attracts, the pattern of differential vulnerability of LHTs to over-exploitation by anglers remains qualitatively unchanged, regardless of the composition of the angler population. Consistent with our aforementioned findings for the biological impacts of consumptive anglers that fish with constant effort, the biological impacts (measured by *SPR*) of dynamic angler populations are greatest to least across LHTs as follows: (again ranked as described above) bull trout, pikeperch/pike, brown trout and perch (Fig. 6).

However, the angler population's composition does alter the quantitative magnitudes of the biological impacts anglers exert on the fished populations. Under liberal *MSLs*, the consumptive angler population reduces *SPR* more than other angler populations across LHTs, whereas under more restrictive *MSLs*, *SPR* is most reduced by the trophy anglers (Fig. 6).

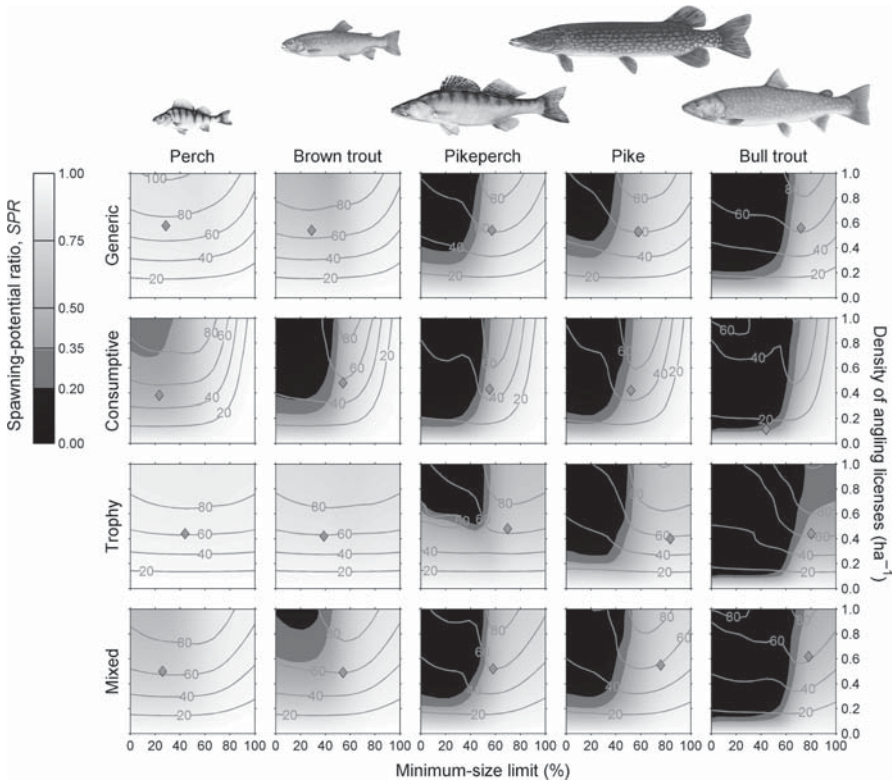


Figure 6 Impacts of fishing, over a range of minimum-size limits (as a percentage of L_{max}), and licence densities, on the spawning-potential ratio (grey contour areas) and on the annual fishing efforts (h ha^{-1}; grey contour curves), across the five considered fish life-history types (columns) and four different populations of angler types (rows); both homogeneous (rows 1–3) and mixed angler populations (row 4; with a composition of 40%:30%:30% generic, consumptive and trophy anglers, respectively). Grey diamonds indicate optimal regulations. All panels are based on considering anglers responding dynamically to the quality of their fishing experience.

Biological impacts on less vulnerable LHTs vary much more among angler populations, despite being generally less severe, than on more vulnerable LHTs. For example, only certain angler populations (consumptive, or consumptive and mixed) overfish perch and brown trout, whereas all angler populations overfish pike, pikeperch and bull trout under some regulations. Across the range of regulations examined, consumptive angler populations reduce the *SPR* below 0.35 more often than other angler populations when targeting pikeperch, perch and brown trout, whereas the trophy-angler population had the greatest impact on bull trout, and impacts on pike are similar for populations of consumptive, trophy and mixed (40%:30%:30%) anglers.

Socially optimal regulations

We also find that socially optimal regulations differ among LHTs: the optimal minimum-size limit MSL_{opt} (measured as a fraction of L_{max}) increases with LHT vulnerability, generally being lowest for perch (23–44% of L_{max}, 9–17 cm), followed by brown trout (29–54%, 15–28 cm), pikeperch (54–70%, 56–72 cm), pike (52–84%, 61–98 cm) and bull trout (44–80%, 43–78 cm; Fig. 7a). In addition, MSL_{opt} varies greatly (over a range wider than 20% of L_{max}) among angler populations (Fig. 7a): for all LHTs except brown trout, MSL_{opt} is highest for trophy-dominated angler populations (composed solely of, or dominated by, trophy anglers) and lowest for consumptive-dominated angler populations (defined analogously). For brown trout, MSL_{opt} is highest for consumptive-dominated angler populations and lowest for generic-dominated angler populations (Fig. 7a). For all LHTs, MSL_{opt} values for all mixed angler populations fall within the ranges predicted for the three homogeneous angler populations.

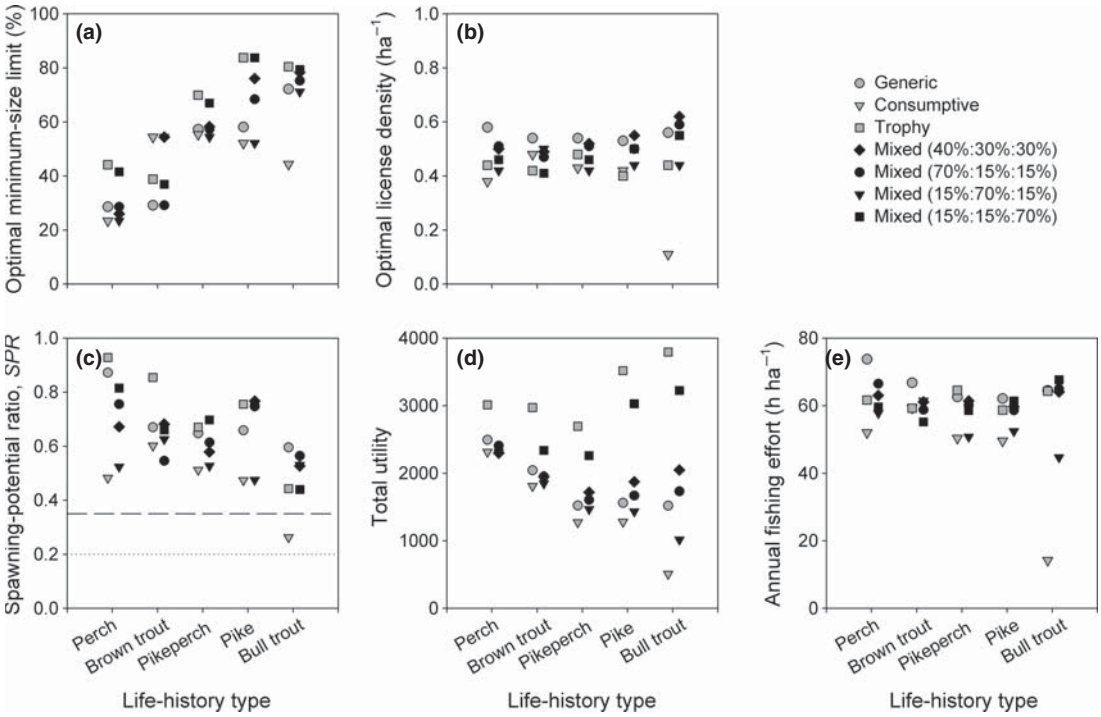


Figure 7 Predicted optimal regulations, and biological and social conditions under these regulations, for the five considered fish life-history types. (a) Optimal minimum-size limit (as a percentage of L_{max}), (b) optimal licence density, (c) spawning-potential ratio *SPR*, (d) total utility and (e) annual fishing effort. Grey symbols correspond to homogeneous angler populations and black symbols to mixed angler populations (with percentages as shown for generic, consumptive and trophy anglers, respectively). In (c), a *SPR* below the dashed line indicates a risk of recruitment overfishing (*SPR* < 0.35) and a *SPR* below the dotted line indicates critical overfishing (*SPR* < 0.20).

Unlike MSL_{opt}, the optimal licence density $A_{L,opt}$ shows no general trend across LHTs, ranging from 0.4 to 0.6 ha^{-1} for most LHTs, but varying by 0.15–0.20 ha^{-1} among angler populations (Fig. 7b). One exception to this pattern occurs for bull trout, for which $A_{L,opt}$ for the consumptive angler population is very low (0.11 ha^{-1}; Fig. 7b). Despite the general consistency of $A_{L,opt}$ across LHTs, the highest $A_{L,opt}$ for pikeperch, perch and brown trout occurs when these LHTs are targeted by a generic angler population, whereas for pike and bull trout, $A_{L,opt}$ is highest for the mixed (40%:30%:30%) angler population (Fig. 7b). On the other extreme, $A_{L,opt}$ for pike and brown trout is lowest when exploited by trophy-dominated angler populations, while for pikeperch, perch and bull trout, the consumptive-dominated angler populations have the lowest $A_{L,opt}$. Thus, unlike MSL_{opt}, $A_{L,opt}$ for mixed angler populations can exceed the range predicted for homogeneous angler populations.

Conditions under socially optimal regulations

Under socially optimal regulations (MSL_{opt} and $A_{L,opt}$), which maximized anglers' total utility, fish populations are generally not at risk of recruitment overfishing. The *SPR* remains above 0.35 across all LHTs and angler populations, except when bull trout is exploited by solely consumptive anglers (in which case *SPR* drops to 0.26; Fig. 7c). However, *SPR* under optimal regulations tends to be lower for LHTs that are generally more vulnerable, although it varies substantially among angler populations (Fig. 7c). Across LHTs, *SPR* is generally lowest for the solely consumptive angler population, except for brown trout, for which the mixed angler population skewed towards generic anglers has the lowest *SPR* (Fig. 7c). The trophy-dominated angler populations reduce the *SPR* of pikeperch, perch and brown trout the least under optimal regulations, while the mixed (40%:30%:30%) angler population had the least impact on

pike, and the generic angler population had the least impact on bull trout (Fig. 7c).

The maximum total utility gained by an angler population varies with LHT and angler population. Under socially optimal regulations, trophy-dominated angler populations gain the most total utility and consumptive-dominated angler populations the least, across LHTs (Fig. 7d). Total utility tends to be higher and vary less for less vulnerable LHTs than for more vulnerable LHTs (Fig. 7d), revealing distinct angler-type-specific LHT preferences. While total utility is high for all angler populations exploiting perch and brown trout, the total utility gained by trophy-dominated angler populations tends to increase with LHT vulnerability, being highest for bull trout and pike. By contrast, the total utility gained by generic-dominated and consumptive-dominated angler populations is highest for perch and brown trout and tends to decline with LTH vulnerability (Fig. 7d).

The annual fishing efforts that the modelled fisheries attract under optimal regulations are reasonable, when compared with the corresponding ranges reported for the different LHTs in the literature [e.g. yellow perch (*Perca flavescens*, Percidae) 3–109 h ha^{-1} (Isermann *et al.* 2005), pike 38–91 h ha^{-1} (Pierce *et al.* 1995) and walleye (*Sander vitreus*, Percidae) 29–112 h ha^{-1} (Beard *et al.* 2003)], potentially being on the high side for some LHTs [e.g. bull trout, 10–20 h ha^{-1} (Post *et al.* 2003)]. Like $A_{L,opt}$, optimal fishing efforts show little variation among LHTs (45–70 h ha^{-1} for most LHTs), but vary more markedly among angler populations (Fig. 7e). Consequently, optimal fishing effort shows little relationship with LHT vulnerability, only differing substantially (14.2 h ha^{-1}) for the consumptive angler population targeting bull trout. Across most LHTs, consumptive-dominated angler populations fish less than the other angler populations under optimal regulations, except for the trophy-dominated angler populations fishing for brown trout (Fig. 7e). Pike, perch and brown trout attract the most fishing effort from generic-dominated angler populations, whereas trophy-dominated angler populations fish more for pikeperch and bull trout (Fig. 7e). The optimal fishing efforts of mixed angler populations generally fall within the range predicted for the three homogeneous angler populations.

The relative participation of different angler types in the mixed angler populations shows clear trends in relation to LHTs under optimal regulations (Fig. 8). These trends occur despite differences among mixed angler populations in MSL_{opt} and $A_{L,opt}$, as well as in the conditions associated with optimal regulations (e.g. total utility and fishing effort). Regardless of LHT, generic anglers tend

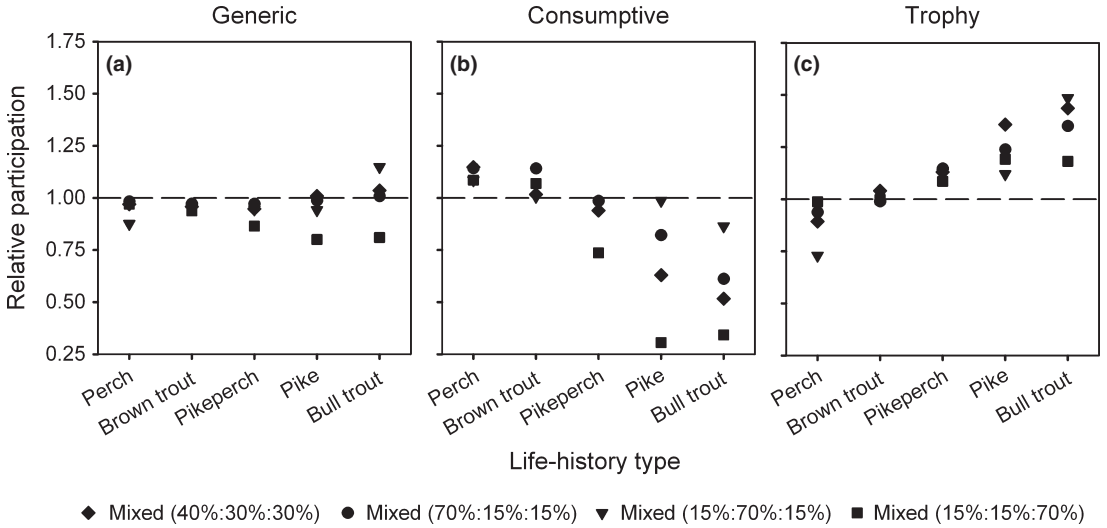


Figure 8 Relative participation, under optimal regulations, of the three considered angler types – (a) generic, (b) consumptive and (c) trophy anglers – in four mixed angler populations (indicated by differently shaped symbols) targeting one of the five considered fish life-history types. Here, relative participation is defined (Table A1, Equation 7c) as the ratio between the proportion of the fishing effort attributed to an angler type, and the corresponding proportion of that angler type in the mixed angler population.

to be underrepresented or proportionally represented in the total angling effort compared with their relative abundance in the mixed angler population (ca. 1; Fig. 8a). By contrast, the relative participation of consumptive anglers decreases (Fig. 8b), and the relative participation of trophy anglers increases (Fig. 8c), as LHT vulnerability increases. Thus, consumptive anglers tend to be overrepresented when fishing for perch and brown trout and underrepresented when fishing for pike, pikeperch and bull trout, whereas trophy anglers show the opposite pattern, being systematically attracted to the larger-bodied LHTs.

Sensitivity analyses

We find that MSL_{opt} is generally less sensitive to changes in life-history parameters than $A_{L,opt}$ (Tables S5 and S6) and that both are most sensitive to changes in age-at-maturation a_m, maximum growth increment h_{max} and instantaneous natural mortality rate m_{na} (note, however, that because the change in a_m is ±1 year, the relative change in a_m is much greater than ±10%). Sensitivity varies across combinations of LHT and angler type. The robustness of MSL_{opt} and $A_{L,opt}$ tends to decrease with LHT vulnerability (e.g. fewer relative changes exceeding 10% for perch compared with bull trout). The sensitivity of MSL_{opt} is relatively similar among angler types, whereas, across all LHTs, $A_{L,opt}$ is more sensitive to changes in life-history parameters when exploited by consumptive anglers, followed by trophy anglers and generic anglers.

Despite the sensitivity of optimal regulations to changes in life-history parameters, predictions about the biological sustainability of the fishery under optimal regulations are fairly robust (Table S7). For pike and pikeperch under optimal regulations, the *SPR* never drops below 0.35. For perch and brown trout under optimal regulations, consumptive anglers reduce *SPR* below 0.35 when age-at-maturation a_m is increased, but remains above 0.35 in all other cases. Similar to our main results, bull trout under optimal regulations cannot biologically sustain exploitation by consumptive anglers, except when the natural mortality rate m_{na} is decreased. Angling of bull trout by generic and trophy anglers also results in *SPR* values below 0.35 when a_m is increased, but remains above 0.35 in all other cases involving those angler types.

Discussion

Here, we have used a novel bioeconomic model developed by Johnston *et al.* (2010) to integrate fish life-history diversity, angler diversity and dynamics and input and output regulations, to evaluate the importance of jointly considering these components for determining optimal regulations and the vulnerability of different fish LHTs to recreational overfishing. Our study is the first to systematically investigate the response of different LHTs in an integrated framework using realistic assumptions about distinct angler types and their dynamic responses to changes in fishing quality. Therefore, our study addresses recent calls for more integrative analyses in recreational fisheries (Fenichel *et al.* 2012).

We find that LHTs are crucially important for determining the vulnerability of recreational fish populations to recruitment overfishing. LHTs differentially affect the fishing-participation decisions of angler types. We also find that because angler types differ in their effort dynamics and fishing practices, the angler population's composition influences the biological impacts of fishing on LHTs. These complex feedbacks between fish LHTs and angler populations result in large variations, across both LHTs and angler populations, in regulations that maximize social welfare. For example, more vulnerable LHTs in our model tend to have higher optimal maximum-size limits MSL_{opt} than less vulnerable LHTs, and as a second example, trophy anglers generally prefer the highest MSL_{opt} for a given LHT, while consumptive anglers prefer the lowest. Yet, despite differences in regulations that achieved optimal social yield OSY, our model predicts optimal regulations to result in biologically sustainable exploitation for all LHTs, except when bull trout are exploited solely by consumptive anglers. A management approach based on social objectives (e.g. OSY), rather than one based solely on biological objectives (e.g. maximum sustainable yield), can thus facilitate biologically sustainable exploitation. This is because biological objectives are inherently part of the social-welfare metric, through their effects on catch-related utility attributes.

Results of our study underscore the importance of considering all three components of a recreational fishery – LHTs, angler types and management regulations – in an integrated framework when predicting sustainable management strategies

for recreational fisheries. Simplification of any of these components may lead to erroneous predictions about fish-angler dynamics, which may result in socially suboptimal management and/or biological collapse.

LHT vulnerability to overfishing

Life-history traits are important for determining the vulnerability of fish populations to overfishing (Reynolds *et al.* 2001; Rose *et al.* 2001; Winemiller 2005). Thus, it is not surprising we have found differences in the susceptibility of LHTs to recreational exploitation. Numerous studies suggest that fish with certain life-history characteristics (i.e., late maturation, large maximum size, low population growth rate) are prone to experience greater population declines from fishing than others (Jennings *et al.* 1998; Reynolds *et al.* 2001; Dulvy *et al.* 2003); our model-based results are in general agreement with those empirical findings.

Specifically, we find that the naturally less abundant and large-bodied LHTs in our model (bull trout, pikeperch and pike) experience more severe population declines in response to recreational angling than the naturally more abundant and smaller-bodied LHTs (perch and brown trout) which can sustain greater fishing mortality. In fact, in agreement with warnings by Post *et al.* (2003) about the extreme susceptibility of bull trout to overfishing, we find that bull trout requires *MSL*s approaching complete catch-and-release fishing, to sustain even low fishing efforts. Thus, our results corroborate other studies (Jennings *et al.* 1998; Reynolds *et al.* 2001; Dulvy *et al.* 2003) suggesting that maximum body size is correlated with vulnerability to over-exploitation by fishing. Furthermore, our results show that indicators such as unexploited abundance, maximum recruitment and potentially also size-at-maturation (although this may simply be a correlate of maximum body size) could also be useful for identifying fish populations susceptible to overfishing, where information on those indicators is available. Moreover, our results suggest that age-at-maturation, fecundity and natural mortality are not likely to be good indicators of vulnerable LHTs, contrary to earlier suggestions (Jennings *et al.* 1998; Reynolds *et al.* 2001).

The differences among LHTs in vulnerability to overfishing relate in part to their overall productivity and their abilities to compensate for fishing-related mortality through density-dependent gains in survivorship and/or reproductive success (Rose *et al.* 2001). This ability depends on species' life-history characteristics and on the strength and frequency of the density-dependent processes to which they are adapted (Rose *et al.* 2001; Winemiller 2005; Goodwin *et al.* 2006). For example, density-dependent survival during early life stages, which is common in many fish species (Myers *et al.* 1995), influences a population's ability to offset fishing mortality (Rose *et al.* 2001; Goodwin *et al.* 2006; Lorenzen 2008). At high population densities, even overcompensation can occur (e.g. in the form of a Ricker stock–recruitment relationship), owing to cannibalism, density-dependent disease transmission or spawning interference (Ricker 1954a; Hilborn and Stokes 2010). This means that with reductions in spawning, stock recruitment initially rises before declining (Hilborn and Stokes 2010). In our model, perch experiences large gains in recruitment because of overcompensation when egg production is reduced by fishing, ultimately resulting in an increase in population density. Overcompensation and cannibalism have been reported for this species (Ohlberger *et al.* 2011). Overcompensation for low fishing mortality also occurs for brown trout, but not when fishing effort, and thus mortality, increases under liberal *MSL*s. All other LHTs, even highly fecund pikeperch, are unable to replace, through compensatory population growth, individuals removed by fishing. In addition to this relatively low compensatory potential, the greater vulnerability of these naturally less abundant and larger-bodied LHTs to over-exploitation reflects the low maximum recruitment and population density (Table 1) of these top predators relative to perch and brown trout.

When considered alone, stock–recruitment relationships can underestimate population responses to fishing (Rochet *et al.* 2000; Rose *et al.* 2001; Rose 2005), even though they strongly influence the compensatory potential of exploited populations, because other density-dependent processes may co-determine those responses (Rose *et al.* 2001; Rose 2005; Lorenzen 2008). For example, density-dependent growth, which is included in our model, can alter a population's compensatory potential, because fish size influences fecundity, maturation and survival (Rose *et al.* 2001; Rose 2005; Lorenzen 2008). However, stock–recruitment relationships are likely more important than

density-dependent growth for determining the compensatory potential of heavily exploited populations (Lorenzen 2008). Indeed, the reductions in biomass and *SPR* we observe across LHTs in our model underscore that density-dependent changes in size-at-age cannot compensate fully for density losses caused by high fishing mortality. Density-dependent changes in fecundity, maturation and reproductive frequency and fisheries-induced evolutionary changes are not considered in our study, but could also be important for determining a fish population's response to exploitation (Rochet *et al.* 2000; Rose *et al.* 2001; Jørgensen *et al.* 2007). We therefore recommend that model extensions aim at including all salient processes influencing a population's compensatory potential.

It has been suggested that, in the absence of detailed information, qualitative 'rules of thumb' based on the life-history characteristics of exploited fish populations could aid fisheries managers in identifying those populations that are most vulnerable to overfishing (Reynolds *et al.* 2001; Winemiller 2005). For example, according to Winemiller and Rose's (1992) classification scheme, 'periodic strategists' (featuring high fecundity, late maturation and low juvenile survival) are predicted to exhibit the highest resilience to fishing, whereas 'equilibrium strategists' (with low fecundity, late maturation and high juvenile survival) should have lower resilience (Winemiller and Rose 1992; Winemiller 2005). Our results regarding the extreme vulnerability of bull trout, a salmonid likely classified as intermediate between periodic and equilibrium strategists (Winemiller and Rose 1992), and indeed its current status – 'vulnerable' in the IUCN's Red List (Gimenez Dixon 1996), and 'threatened' in coterminous USA (US Fish and Wildlife Service 2010), provide some support for these predictions, as do our findings related to pike, pikeperch, perch and brown trout, which are all broadly classified as periodic strategists (Rose *et al.* 2001; Vila-Gispert and Moreno-Amich 2002) and are all listed as species of least concern (Freyhof and Kottelat 2008a,b,c; Freyhof 2011).

However, our results caution that coarse life-history classifications, such as Winemiller and Rose's (1992), risk obscuring important life-history differences that exist within the broadly defined strategies (Rose *et al.* 2001): as we have shown here, these life-history differences can substantially influence vulnerability to over-exploitation. For example, despite four of our LHTs being classified as periodic strategists (Vila-Gispert and Moreno-Amich 2002), we found pike and pikeperch to be much more vulnerable to recruitment overfishing than brown trout or perch. Indeed, pike and walleye, a congeneric of pikeperch, have been shown to be highly vulnerable to over-exploitation by recreational angling (e.g. Post *et al.* 2002). Declines in brown-trout stocks as a result of recreational fishing have also been documented (e.g. Almodóvar and Nicola 2004). Thus, in the absence of more detailed information, body size and life-history classification can provide directions for identifying LHTs vulnerable to overfishing. However, the present study and other work (Rose 2005; Coggins *et al.* 2007) suggest that, where possible, a quantitative modelling approach should be used to provide more robust predictions about the response of different LHTs to recreational angling.

Angler dynamics

When predicting the impacts of recreational fishing, one needs to consider not only fish life history but also the preferences and dynamics of anglers utilizing a fishery (Post *et al.* 2003; Johnston *et al.* 2010). Our results show that dynamic angler behaviour, regardless of angler type, does not alter the general trend in vulnerability to recruitment overfishing across LHTs our model predicts for constant consumptive fishing effort: with and without dynamic angler behaviour, bull trout are most vulnerable and perch are least vulnerable to fishing-induced *SPR* declines. Yet, the composition of the angler population and its effort dynamics are important for determining the magnitude of the impact angling has on LHTs in our model.

We find that differences in fishing practices (skill levels, propensity for voluntary catch-and-release, fish size targeted; Table S3) among angler types influence catch and harvest rates. Under liberal *MSLs*, consumptive anglers have greater impacts than other anglers types on less vulnerable LHTs in our model (perch and brown trout), because catch rates of these naturally abundant LHTs (e.g. maximum 11.3, 20.0, 15.0 harvestable-sized perch per day and 5.5, 8.6, 7.7 harvestable-sized brown trout per day for generic, consumptive and trophy anglers, respectively) are generally high, and consumptive anglers harvest all legal-sized fish caught (i.e., fish are not voluntarily released).

On the other hand, trophy anglers in our model, while also enjoying high catch rates, only harvest one fish every second day. Thus, a large disparity in harvest rates results among angler types. By contrast, catch rates of naturally less abundant LHTs, bull trout and pike in our model (with a maximum of 0.17, 0.19, 0.14 harvestable-sized bull trout per day and 0.55, 0.75, 0.80 harvestable-sized pike per day for generic, consumptive, and trophy anglers, respectively) are generally low and thus do not allow a similar disparity in harvest rates to develop. In our model, catch rates of harvestable fish often do not exceed even the conservative personal daily harvest limits set by trophy anglers, similar to reports for regulated daily bag limits (Cook *et al.* 2001). This implies that regulated daily bag limits may also have little effect, unless they are low enough to be achieved. Voluntary release by any angler type rarely occurs in our model and therefore is less important for determining the fishing impacts on the more vulnerable LHTs. Instead, the variation in the impact of anglers on those more vulnerable LHTs emerges through differences in angler behaviour and thus fishing effort.

In addition to harvesting practices, dynamic angler behaviour also determines angling impacts on LHTs. First, regardless of angler type, and despite substantial declines in fish abundances and catch rates under liberal harvest regulations, some anglers continued to be attracted to the modelled fishery. This has the potential to collapse fisheries (Post *et al.* 2002), demonstrating the importance of considering multi-attribute angler behaviour in recreational fisheries models (see also Johnston *et al.* 2010), rather than assuming that catch rates alone dictate the fishing decisions of anglers (e.g. Cox *et al.* 2003). Second, our results show how differences in behaviour among angler populations, because of angler-type-specific fishing preferences, alter angling impacts, in some cases leading to counterintuitive outcomes. For example, despite the tendency of trophy anglers to practice voluntary catch-and-release (Arlinghaus *et al.* 2007), across LHTs, populations of trophy anglers reduce the *SPR* more than other angler populations under moderate to restrictive *MSLs*. This reflects that more specialized anglers often prefer or tolerate restrictive harvest regulations (Aas *et al.* 2000; Oh and Ditton 2006; Arlinghaus *et al.* 2007) and respond to them differently than other anglers (Beard *et al.* 2003). Thus, under constrained harvest conditions, while the angling efforts by consumptive and generic anglers declined, in our models, effort by trophy anglers remains high, resulting in trophy anglers killing more fish than other angler types. In some cases, this mortality is sufficient to put populations at risk of recruitment overfishing (e.g. for bull trout with licence densities exceeding 0.7 ha^{-1}), even under total catch-and-release regulations.

Our results thus support claims that discard mortality can substantially impact the biological sustainability of some fisheries (Coggins *et al.* 2007). In combination, the fishing practices and fishing preferences of trophy anglers, counterintuitively, result in their having the greatest overall impact on bull trout among all studied angler populations. These findings highlight that, to prevent unexpected results, managers and researchers need to better understand the types of anglers utilizing a fishery, as well as the dynamics resulting from their differential practices and preferences, to achieve more robust predictions about recreational-fishing impacts. Where sufficient information is available, our modelling approach can be used to explore implications of management changes prior to their enactment, so as to help select practically implemented management changes based on their efficacy.

Optimal management

In our model, differences in LHT vulnerability and fish-angler interactions influence the regulations that maximize an angler population's total utility, measured in terms of OSY. For example, although the optimal density $A_{L,opt}$ of licences does not show a general trend with LHT vulnerability, MSL_{opt} has a strong tendency to increase with LHT vulnerability (with MSL_{opt} being generally most liberal for perch and most restrictive for bull trout).

Minimum-size limits are often set in recreational fisheries to be as low as possible (so as to maximize harvest) while allowing fish to spawn at least once (Johnson and Martinez 1995; Diana and Smith 2008). This tactic, however, may not be appropriate for all species. Whereas low *MSLs* may be suitable for perch, *MSLs* for pike – set at, for example, 46–76 cm in North America (Paukert *et al.* 2001) – are often below, or at the lower margin of, the range of MSL_{opt} predicted by our model (61–98 cm). Our findings thus suggest that species-specific considerations when setting *MSLs* could gen-

erate greater social benefits from a fishery, supporting concerns that 'one size fits all' policies may erode ecological and social resilience (Carpenter and Brock 2004). The increase in MSL_{opt} with vulnerability suggests that unexploited abundance, maximum recruitment, maximum body size and potentially also size-at-maturation (if known) can aid managers in setting more socially advantageous *MSLs*, because of the correlation of those indicators with vulnerability.

Accounting not only for LHTs but also angler diversity, however, is crucially important when establishing management regulations (Radomski *et al.* 2001; Johnston *et al.* 2010). In agreement with findings that more specialized anglers are more tolerant of restrictive harvest regulations (Aas *et al.* 2000; Oh and Ditton 2006), MSL_{opt} in our model, as a general rule, tends to be lowest for consumptive-dominated angler populations and highest for trophy-dominated angler populations. However, in the case of brown trout, consumptive-dominated angler populations have the highest MSL_{opt}, whereas generic-dominated angler populations have the lowest. The reason for this finding is that the greater harvest orientation and skill level of consumptive anglers relative to generic anglers require a higher *MSL* to maintain a sustainable fishery for consumptive anglers. On the other hand, the less-consumptive generic anglers can fish with high effort under the more liberal harvest regulations they preferred, because of the relatively productive nature of brown trout.

Angler population composition is also important for determining the optimal density $A_{L,opt}$ of licences, including subtle interactions with LHT differences. For example, we find that the generic angler population exhibit the highest $A_{L,opt}$ when LHT vulnerability is low, whereas mixed angler populations have an even higher $A_{L,opt}$ when LHT vulnerability is high (as it is, e.g., for pike and bull trout). This result highlights the importance of considering the complex interplay among angler types within an angler population.

More broadly, our findings support suggestions that managing for diverse angling opportunities could better conserve fish populations and increase the social welfare provided by a fishery (e.g. Aas *et al.* 2000; Carpenter and Brock 2004; Johnston *et al.* 2010). Given that angler types generally display consistent preferences for optimal regulations, some knowledge of the angler population could assist managers with meeting this challenge. However, as our previously discussed results underscore, management decisions should be based on both the life history of an exploited fish population and the diversity of interests in the corresponding angler population (e.g. Diana and Smith 2008).

Of relevance for managers faced with the challenge of maximizing angler satisfaction and participation while maintaining a viable fishery (Radomski *et al.* 2001; Cox and Walters 2002; Peterson and Evans 2003) is our promising result that adopting a socially optimal approach (based on OSY) to recreational fisheries management achieves both objectives. Specifically, *SPR* in our model is maintained above 0.35 except for bull trout, a LHT that because of its extreme vulnerability to overfishing cannot biologically sustain a satisfied solely consumptive angler population under optimal regulations. In most cases, however, managing for OSY is more likely to achieve management objectives and result in lower fishing mortality than managing for maximum sustainable yield (Radomski *et al.* 2001), because a viable recreational fishery provides social and cultural benefits that are not measured by yield alone (Roedel 1975; Malvestuto and Hudgins 1996). Notwithstanding these findings, given the decrease in *SPR* that occurs in our model with increased LHT vulnerability under optimal regulations, a precautionary approach should be adopted when setting optimal regulations for naturally more vulnerable LHTs.

Emergent LHT preferences

A final key finding of this study is the emergent preferences of angler types for particular LHTs. For example, generic and consumptive angler populations tend to gain more total utility from less vulnerable LHTs than from more vulnerable LHTs, creating an emergent preference for the naturally more abundant and smaller-bodied LHTs. By contrast, the total utility of populations of trophy anglers tends to increase with LHT vulnerability, creating an emergent preference for the naturally less abundant and larger-bodied LHTs. These trends occur despite standardizing anglers' PWU baseline expectations for life-history differences in fish size and abundance. The social welfare provided by perch is high for all angler populations, because perch can maintain high relative catch rates even when fishing mortality is high under liberal *MSLs*. However, relatively low catch rates

and aversions to restrictive regulations made the more vulnerable LHTs (pike, pikeperch and bull trout) less attractive to consumptive or generic anglers. Trophy anglers, by contrast, prefer the naturally less abundant and larger-bodied bull trout and pike, because of their tolerance for restrictive regulations and their ability to catch relatively larger fish. The greater average and maximum relative size achieved for these LHTs likely results from stronger density dependence in growth and reduced truncation of the size distribution under restrictive *MSLs*. These novel findings suggest that the intrinsic life history of fish populations strongly influence which species or LHTs an angler type prefers. Indeed, in support of these results, Beardmore *et al.* (2011) found that more specialized, trophy-oriented German anglers were particularly attracted to larger-bodied species such as pike.

One implication of angler-type-specific LHT preferences is that the socially optimal management of a given recreational fishery may systematically exclude or attract certain angler types. For example, as LHT vulnerability increases, the relative participation of trophy anglers in our modelled mixed angler populations under optimal regulations also increases, and the reverse is true for consumptive anglers. These trends occur despite large differences in the optimal regulations underlying them. Therefore, depending on the social welfare measure used (Johnston *et al.* 2010), managing for OSY may come at a greater cost to certain angler types than others, which might lead to conflict among different segments of the angling community (Loomis and Ditton 1993; Arlinghaus *et al.* 2007). However, our modelling approach can be used by managers to identify likely conflict situations, and it provides them with a tool for transparently illustrating the benefits of regulation changes to the angler community as a whole. Furthermore, understanding which angler types will be attracted to specific LHTs will aid managers in setting appropriate socially optimal regulations.

Limitations and extensions

While the present study provides important insights into the interplay between fish populations, anglers and management measures, there are several limitations to our work, and resultant opportunities for extensions, that deserve to be highlighted. A first set is related to angler dynamics, while a second set is related to fish dynamics; we now discuss these in turn.

First, our model constitutes a single-species, single-lake model omitting a regional perspective and multispecies interactions. Movement among various fisheries in a landscape (Post *et al.* 2008; Hunt *et al.* 2011; Post and Parkinson 2012), or a multispecies fishery (Worm *et al.* 2009), could affect the outcomes presented here. Extending our model to include multispecies interactions or a spatial component of lakes connected by mobile anglers would be interesting avenues to pursue in future studies.

Second, by standardizing the baseline expectations of angler types for LHT differences in body size and abundance, we have assumed that angler-type-specific PWU functions are identical across LHTs. However, although B. Beardmore, W. Haider, L.M. Hunt and R. Arlinghaus (unpublished data) found no significant differences in the relative preferences (e.g., standardized for catch rate and body size) of different German angler types for several species, it is still possible that the preferences of angler types may differ among species. Species-specific or even regional differences in the utility functions of anglers could result in lower fishing effort under optimal regulations than those predicted in this study.

Third, we did not include inverse density-dependent catchability in our model. The existence of such a relationship could strongly affect the threshold effort that leads to severe overfishing (Hunt *et al.* 2011). Thus, the omission of density-dependent catchability may make our model results overly optimistic, by underestimating the risk of collapse for some species.

Fourth, other harvest regulations, such as daily bag limits, could potentially alter our study's predictions, by minimizing the disparity in fishing mortality imposed by different angler types. For example, our model may overemphasize the fishing impacts of consumptive anglers relative to other angler types, because the former are assumed to harvest all fish caught. However, this bias would only be relevant for the less vulnerable LHTs examined here, for which catch rates greatly exceed voluntary-release thresholds, and moreover, only when regulated bag limits are set low enough that catch rates can exceed them with sufficient frequency. For example, in many places anglers are allowed to harvest as many as 25 yellow perch per day, or even more (Isermann *et al.* 2007), while the maximum achieved catch rate in

our model was 21.5 fish per day. For the more vulnerable LHTs we have examined, angler types rarely manage to catch even the most conservative daily quota (personal or regulated), resulting in harvest rates that are similar among angler types. Thus, as suggested in the literature (Cook *et al.* 2001), anglers are often not limited by daily bag limits: they harvest less fish than their daily bag limit would allow, either because they voluntarily choose not to harvest so many fish or because they do not manage to catch their daily limit. Nevertheless, the inclusion of daily bag limits might still alter the effort dynamics of anglers in our model, either through regulation aversions (Beard *et al.* 2003) or through resultant changes in fish population dynamics, which would therefore make an interesting extension for future research.

Other limitations of our model relate to fish dynamics. First, our results are based on the parameterization of a single-species system without any consideration of food-web interactions. Thus, for more realistic predictions about a specific fishery, the model will need to be calibrated appropriately. However, the purpose of this work has been to encompass a range of LHTs experienced by anglers, rather than to model any one specific population.

Second, as previously highlighted, some realistic density-dependent processes resulting from phenotypic plasticity (e.g. in maturation), which could be important for determining a LHT's compensatory (Rochet *et al.* 2000) potential and thus its predicted vulnerability, were not included in our model. In addition, we did not account for any harvest-induced evolutionary changes in life-history traits (e.g., Jørgensen *et al.* 2007) that might influence a species' response to fishing, for example, through changes in its reproductive ecology (Enberg *et al.* 2010). Plastic or genetic changes that result in earlier maturation at smaller sizes, for example, could allow a fish population to withstand higher fishing pressure, especially the larger-bodied, more vulnerable LHTs. Such changes would often also influence angler behaviour, by altering the perceived quality of a fishery, for example, if mean fish size declined.

Third, unaccounted changes in demographic structure, through juvenescence or size-dependent maternal effects, could alter reproductive potential and population stability (Anderson *et al.* 2008; Arlinghaus *et al.* 2010; Hsieh *et al.* 2010). Size-dependent maternal effects would likely have more of an influence on LHTs that have lower proportions of adults in the population and fewer first-time spawners in the mature population (e.g. bull trout; Table 1), as well as on the more vulnerable LHTs. The impacts reported here are likely to be conservative if large females are preferentially removed by fishing and size-dependent maternal effects impair recruitment at low fish population abundance.

The influences of phenotypic plasticity, fisheries-induced evolution and maternal effects on predictions about optimal regulations would be fascinating to examine, but were beyond the scope of the present study. Future research should also investigate alternative regulations, for example, slots-length limits designed to protect large spawners (Arlinghaus *et al.* 2010).

Conclusions

Our study, to our knowledge, is the first to use an integrated modelling approach, based on theories from ecology, economics and human-dimensions research, to systematically investigate how fish life-history and angler types influence the vulnerability of fish populations to recreational overfishing and the behaviour of angler populations exploiting them. Using such an approach has revealed some unexpected results and some general patterns that could not have been exposed if the interplay between fish populations, anglers and management measures had not been considered. We have also shown that socially optimal management generally achieves both social and biological sustainability, a result that can be taken as encouraging for recreational fisheries managers. In combination, our results demonstrate the benefit of integrating the traditionally separate fields of fisheries ecology and social sciences to facilitate the sustainable management of recreational fisheries. In this context, our results caution that managing all species according to the same rationale may result in the loss of social welfare and put fish populations at risk of over-exploitation.

Acknowledgements

We thank H. Winkler for pikeperch information and M. Allen and one anonymous reviewer for constructive comments on this manuscript. Financial support was provided by the Gottfried-Wilhelm-Leibniz Community through the Adaptfish

Project (www.adaptfish.igb-berlin.de). RA received additional funding by the German Ministry for Education and Research (BMBF) through the Program for Social-Ecological Research Besatzfisch-Project (grant no. 01UU0907, www.besatz-fisch.de). UD gratefully acknowledges financial support by the European Commission, through the Marie Curie Research Training Network on Fisheries-induced Adaptive Changes in Exploited Stocks (FishACE, MRTN-CT-2004-005578) and the Specific Targeted Research Project on Fisheries-induced Evolution (FinE, SSP-2006-044276) under the European Community's Sixth Framework Program. UD received additional support by the European Science Foundation, the Austrian Science Fund, the Austrian Ministry of Science and Research and the Vienna Science and Technology Fund.

References

Aas, Ø., Haider, W. and Hunt, L. (2000) Angler responses to potential harvest regulations in a Norwegian sport fishery: a conjoint-based choice modeling approach. *North American Journal of Fisheries Management* **20**, 940–950.

Allen, M.S., Brown, P., Douglas, J., Fulton, W. and Catalano, M. (2009) An assessment of recreational fishery harvest policies for Murray cod in southeast Australia. *Fisheries Research* **95**, 260–267.

Almodóvar, A. and Nicola, G.G. (2004) Angling impact on conservation of Spanish stream-dwelling brown trout *Salmo trutta*. *Fisheries Management and Ecology* **11**, 173–182.

Anderson, C.N.K., Hsieh, C.H., Sandin, S.A. *et al.* (2008) Why fishing magnifies fluctuations in fish abundance. *Nature* **452**, 835–839.

Arlinghaus, R. (2004) *A Human Dimensions Approach Towards Sustainable Recreational Fisheries Management*. Turnshare Ltd., London.

Arlinghaus, R., Cooke, S.J., Lyman, J. *et al.* (2007) Understanding the complexity of catch-and-release in recreational fishing: an integrative synthesis of global knowledge from historical, ethical, social and biological perspectives. *Reviews in Fisheries Science* **15**, 75–167.

Arlinghaus, R., Johnson, B.M. and Wolter, C. (2008) The past, present and future role of limnology in freshwater fisheries science. *International Review of Hydrobiology* **93**, 541–549.

Arlinghaus, R., Matsumura, S. and Dieckmann, U. (2009) Quantifying selection differentials caused by recreational fishing: development of modeling framework and application to reproductive investment in pike (*Esox lucius*). *Evolutionary Applications* **2**, 335–355.

Arlinghaus, R., Matsumura, S. and Dieckmann, U. (2010) The conservation and fishery benefits of protecting large pike (*Esox lucius* L.) by harvest regulations in recreational fishing. *Biological Conservation* **143**, 1444–1459.

Beamesderfer, R.C.P. and North, J.A. (1995) Growth, natural mortality, and predicted response to fishing for largemouth bass and smallmouth bass populations in North America. *North American Journal of Fisheries Management* **15**, 688–704.

Beard, T.D. Jr, Cox, S.P. and Carpenter, S.R. (2003) Impacts of daily bag limit reductions on angler effort in Wisconsin walleye lakes. *North American Journal of Fisheries Management* **23**, 1283–1293.

Beardmore, B., Haider, W., Hunt, L.M. and Arlinghaus, R. (2011) The importance of trip context for determining primary angler motivations: are more specialized anglers more catch-oriented than previously believed? *North American Journal of Fisheries Management* **31**, 861–879.

Beverton, R.J.H. and Holt, S.J. (1957) On the dynamics of certain North Sea fish populations.*Fishery Investigations Series II*, Vol. 19. U.K. Ministry of Agriculture, Fisheries and Food, London, 533 pp.

Bryan, H. (1977) Leisure value systems and recreational specialization: the case of trout fishermen. *Journal of Leisure Research* **9**, 174–187.

Carpenter, S.R. and Brock, W.A. (2004) Spatial complexity, resilience, and policy diversity: fishing on lake-rich landscapes. *Ecology and Society* **9**, 8 [online]. Available at: www.ecologyandsociety.org/vol9/iss1/art8/ (accessed 1 October 2008).

Clark, W.G. (2002) F35% revisited ten years later. *North American Journal of Fisheries Management* **22**, 251–257.

Cochrane, K.L. (2000) Reconciling sustainability, economic efficiency and equity in fisheries: the one that got away? *Fish and Fisheries* **1**, 3–21.

Coggins, L.G. Jr, Catalano, M.J., Allen, M.S., Pine, W.E. III and Walters, C.J. (2007) Effects of cryptic mortality and the hidden costs of using length limits in fishery management. *Fish and Fisheries* **8**, 196–210.

Coleman, F.C., Figueira, W.F., Ueland, J.S. and Crowder, L.B. (2004) The impact of United States recreational fisheries on marine fish populations. *Science* **305**, 1958–1960.

Cook, M.F., Goeman, T.J., Radomski, P.J., Younk, J.A. and Jacobson, P.C. (2001) Creel limits in Minnesota: a proposal for change. *Fisheries* **26**, 19–26.

Cooke, S.J. and Cowx, I.G. (2004) The role of recreational fisheries in global fish crises. *BioScience* **54**, 857–859.

Cox, S. and Walters, C. (2002) Maintaining quality in recreational fisheries: how success breeds failure in management of open-access sport fisheries. In: *Recreational Fisheries: Ecological, Economic and Social Evalua-*

tion (eds T.J. Pitcher and C.E. Hollingworth). Blackwell Publishing, Oxford, U.K., pp. 107–119.

Cox, S.P., Beard, T.D. and Walters, C. (2002) Harvest control in open-access sport fisheries: hot rod or asleep at the reel? *Bulletin of Marine Science* **70**, 749–761.

Cox, S.P., Walters, C.J. and Post, J.R. (2003) A model-based evaluation of active management of recreational fishing effort. *North American Journal of Fisheries Management* **23**, 1294–1302.

Diana, J. and Smith, K. (2008) Combining ecology, human demands, and philosophy into the management of northern pike in Michigan. *Hydrobiologia* **601**, 125–135.

Dulvy, N.K., Sadovy, Y. and Reynolds, J.D. (2003) Extinction vulnerability in marine populations. *Fish and Fisheries* **4**, 25–64.

Duncan, J.R. and Lockwood, J.L. (2001) Extinction in a field of bullets: a search for causes in the decline of the world's freshwater fishes. *Biological Conservation* **102**, 97–105.

Enberg, K., Jørgensen, C. and Mangel, M. (2010) Fishing-induced evolution and changing reproductive ecology of fish: the evolution of steepness. *Canadian Journal of Fisheries and Aquatic Sciences* **67**, 1708–1719.

Fenichel, E.P., Abbott, J.K. and Huang, B. (2012) Modelling angler behaviour as a part of the management system: synthesizing a multi-disciplinary literature. *Fish and Fisheries*, doi:10.1111/j.1467-2979.2012.00456.x.

Fisher, M.R. (1997) Segmentation of the angler population by catch preference, participation, and experience: a management-oriented application of recreation specialization. *North American Journal of Fisheries Management* **17**, 1–10.

Freyhof, J. (2011) *Salmo trutta*. In: *IUCN 2011. IUCN Red List of Threatened Species.* Version 2011.2. Available at: www.iucnredlist.org (accessed 11 April 2012).

Freyhof, J. and Kottelat, M. (2008a) *Esox lucius*. In: *IUCN 2011. IUCN Red List of Threatened Species*. Version 2011.2. Available at: www.iucnredlist.org (accessed 11 April 2012).

Freyhof, J. and Kottelat, M. (2008b) *Perca fluviatilis*. In: *IUCN 2011. IUCN Red List of Threatened Species*. Version 2011.2. Available at: www.iucnredlist.org (accessed 11 April 2012).

Freyhof, J. and Kottelat, M. (2008c) *Sander lucioperca*. In: *IUCN 2011. IUCN Red List of Threatened Species*. Version 2011.2. Available at: www.iucnredlist.org (accessed 11 April 2012).

Fulton, E.A., Smith, A.D.M., Smith, D.C. and van Putten, I.E. (2011) Human behaviour: the key source of uncertainty in fisheries management. *Fish and Fisheries* **12**, 2–17.

Gabelhouse, D.W. Jr (1984) A length-categorization system to assess fish stocks. *North American Journal of Fisheries Management* **4**, 273–285.

Gimenez Dixon, M. (1996) *Salvelinus confluentus*. In: *IUCN 2011. IUCN Red List of Threatened Species*. Version 2011.2. Available at: www.iucnredlist.org (accessed 11 April 2012).

Goodwin, N.B., Grant, A., Perry, A.L., Dulvy, N.K. and Reynolds, J.D. (2006) Life history correlates of density-dependent recruitment in marine fishes. *Canadian Journal of Fisheries and Aquatic Sciences* **63**, 494–509.

Goodyear, C.P. (1993) Spawning stock biomass per recruit in fisheries management: foundation and current use. In: *Risk Evaluation and Biological Reference Points for Fisheries Management* (eds S.J. Smith, J.J. Hunt and D. Rivard). Canadian Special Publication of Fisheries and Aquatic Sciences **120**, 67–81.

Guy, C.S., Neumann, R.M. and Willis, D.W. (2006) New terminology for proportional stock density (PSD) and relative stock density (RSD) : proportional size structure (PSS). *Fisheries* **31**, 86–87.

Hahn, J. (1991) Angler specialization: measurement of a key sociological concept and implications for fisheries management decisions. *American Fisheries Society Symposium* **12**, 380–389.

Hilborn, R. (2007) Defining success in fisheries and conflicts in objectives. *Marine Policy* **31**, 153–158.

Hilborn, R. and Stokes, K. (2010) Defining overfished stocks: have we lost the plot? *Fisheries* **35**, 113–120.

Hsieh, C.H., Yamauchi, A., Nakazawa, T. and Wang, W.F. (2010) Fishing effects on age and spatial structures undermine population stability of fishes. *Aquatic Sciences* **72**, 165–178.

Hunt, L. (2005) Recreational fishing site choice models: insights and future opportunities. *Human Dimensions of Wildlife* **10**, 153–172.

Hunt, L.M., Arlinghaus, R., Lester, N. and Kushneriuk, R. (2011) The effects of regional angling effort, angler behavior, and harvesting efficiency on landscape patterns of overfishing. *Ecological Applications* **21**, 2555–2575.

Isermann, D.A., Willis, D.W., Blackwell, B.G. and Lucchesi, D.O. (2007) Yellow perch in South Dakota: population variability and predicted effects of creel limit reductions and minimum length Limits. *North American Journal of Fisheries Management* **27**, 918–931.

Isermann, D.A., Willis, D.W., Lucchesi, D.O. and Blackwell, B.G. (2005) Seasonal harvest, exploitation, size selectivity, and catch preferences associated with winter yellow perch anglers on South Dakota lakes. *North American Journal of Fisheries Management* **25**, 827–840.

Jacobson, P.C. (1996) Trophy and consumptive value-per-recruit analysis for a walleye fishery. *North American Journal of Fisheries Management* **16**, 75–80.

Jennings, S., Reynolds, J.D. and Mills, S.C. (1998) Life history correlates of responses to fisheries exploitation. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **265**, 333–339.

Johnson, B.M. and Martinez, P.J. (1995) Selecting harvest regulations for recreational fisheries: opportunities for research/management cooperation. *Fisheries* **20**, 22–29.

Johnston, F.D., Arlinghaus, R. and Dieckmann, U. (2010) Diversity and complexity of angler behaviour drive socially optimal input and output regulations in a bioeconomic recreational-fisheries model. *Canadian Journal of Fisheries and Aquatic Sciences* **67**, 1507–1531.

Johnston, F.D., Arlinghaus, R., Stelfox, J. and Post, J.R. (2011) Decline in angler use despite increased catch rates: anglers' response to the implementation of a total catch-and-release regulation. *Fisheries Research* **110**, 189–197.

Jørgensen, C., Enberg, K., Dunlop, E.S. *et al.* (2007) Managing evolving fish stocks. *Science* **318**, 1247–1248.

Lester, N.P., Shuter, B.J. and Abrams, P.A. (2004) Interpreting the von Bertalanffy model of somatic growth in fishes: the cost of reproduction. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **271**, 1625–1631.

Lewin, W.C., Arlinghaus, R. and Mehner, T. (2006) Documented and potential biological impacts of recreational fishing: insights for management and conservation. *Reviews in Fisheries Science* **14**, 305–367.

Loomis, D.K. and Ditton, R.B. (1993) Distributive justice in fisheries management. *Fisheries* **18**, 14–18.

Lorenzen, K. (2008) Fish population regulation beyond stock and recruitment: the role of density-dependent growth in the recruited stock. *Bulletin of Marine Science* **83**, 181–196.

Mace, P.M. (1994) Relationships between common biological reference points used as thresholds and targets of fisheries management strategies. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 110–122.

Malvestuto, S.P. and Hudgins, M.D. (1996) Optimum yield for recreational fisheries management. *Fisheries* **21**, 6–17.

McPhee, D.P., Leadbitter, D. and Skilleter, G.A. (2002) Swallowing the bait: is recreational fishing in Australia ecologically sustainable? *Pacific Conservation Biology* **8**, 40–51.

Myers, R.A., Barrowman, N.J., Hutchings, J.A. and Rosenberg, A.A. (1995) Population dynamics of exploited fish stocks at low population levels. *Science* **269**, 1106–1108.

Oh, C.O. and Ditton, R.B. (2006) Using recreation specialization to understand multi-attribute management preferences. *Leisure Sciences* **28**, 369–384.

Ohlberger, J., Langangen, Ø., Edeline, E. *et al.* (2011) Stage-specific biomass overcompensation by juveniles in response to increased adult mortality in a wild fish population. *Ecology* **92**, 2175–2182.

Paukert, C.P., Klammer, J.A., Pierce, R.B. and Simonson, T.D. (2001) An overview of northern pike regulations in North America. *Fisheries* **26**, 6–13.

Paul, A.J., Post, J.R. and Stelfox, J.D. (2003) Can anglers influence the abundance of native and nonnative salmonids in a stream from the Canadian Rocky Mountains? *North American Journal of Fisheries Management* **23**, 109–119.

Peterson, J.T. and Evans, J.W. (2003) Quantitative decision analysis for sport fisheries management. *Fisheries* **28**, 10–21.

Pierce, R.B., Tomcko, C.M. and Schupp, D.M. (1995) Exploitation of northern pike in seven small north-central Minnesota lakes. *North American Journal of Fisheries Management* **15**, 601–609.

Pigliucci, M. (2005) Evolution of phenotypic plasticity: where are we going now? *Trends in Ecology and Evolution* **20**, 481–486.

Post, J.R., Mushens, C., Paul, A. and Sullivan, M. (2003) Assessment of alternative harvest regulations for sustaining recreational fisheries: model development and application to bull trout. *North American Journal of Fisheries Management* **23**, 22–34.

Post, J.R. and Parkinson, E.A. (2012) Temporal and spatial patterns of angler effort across lake districts and policy options to sustain recreational fisheries. *Canadian Journal of Fisheries and Aquatic Sciences* **69**, 321–329.

Post, J.R., Persson, L., Parkinson, E.A. and van Kooten, T. (2008) Angler numerical response across landscapes and the collapse of freshwater fisheries. *Ecological Applications* **18**, 1038–1049.

Post, J.R., Sullivan, M., Cox, S. *et al.* (2002) Canada's recreational fisheries: the invisible collapse? *Fisheries* **27**, 6–17.

Radomski, P.J., Grant, G.C., Jacobson, P.C. and Cook, M.F. (2001) Visions for recreational fishing regulations. *Fisheries* **26**, 7–18.

Reynolds, J.D., Jennings, S. and Dulvy, N.K. (2001) Life histories of fishes and population response to exploitation. In: *Conservation of Exploited Species* (eds J.D. Reynolds, G.M. Mace, K.H. Redford and J.G. Robinson). Cambridge University Press, Cambridge, UK, pp. 147–168.

Reynolds, J.D., Webb, T.J. and Hawkins, L.A. (2005) Life history and ecological correlates of extinction risk in European freshwater fishes. *Canadian Journal of Fisheries and Aquatic Sciences* **692**, 854–862.

Ricker, W.E. (1954a) Effects of compensatory mortality upon population abundance. *Journal of Wildlife Management* **18**, 45–51.

Ricker, W.E. (1954b) Stock and recruitment. *Journal of the Fisheries Research Board of Canada* **11**, 559–623.

Rochet, M.J., Cornillon, P.A., Sabatier, R. and Pontier, D. (2000) Comparative analysis of phylogenetic and fishing effects in life history patterns of teleost fishes. *Oikos* **91**, 255–270.

Roedel, P.M. (1975) A summary and critique of the symposium on optimal sustainable yield. In: *Optimum Sustainable Yield as a Concept in Fisheries Management. American Fisheries Society Special Publication*. American Fisheries Society, Bethesda, MD, pp. 79–89.

Rose, K.A. (2005) Lack of relationship between simulated fish population responses and their life history traits: inadequate models, incorrect analysis, or site-specific factors? *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 886–902.

Rose, K.A., Cowan, J.H. Jr, Winemiller, K.O., Myers, R.A. and Hilborn, R. (2001) Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. *Fish and Fisheries* **2**, 293–327.

U.S. Fish and Wildlife Service. (2010) *Species Information: Threatened and Endangered Animals and Plants*. U.S. Fish and Wildlife Service, Washington, DC 20240. Available at: http://ecos.fws.gov/speciesProfile/profile/speciesProfile.action?spcode=E065 (accessed 31 March 2010).

van Poorten, B.T. and Post, J.R. (2005) Seasonal fishery dynamics of a previously unexploited rainbow trout population with contrasts to established fisheries. *North American Journal of Fisheries Management* **25**, 329–345.

Vila-Gispert, A. and Moreno-Amich, R. (2002) Life-history patterns of 25 species from European freshwater fish communities. *Environmental Biology of Fishes* **65**, 387–400.

Wilberg, M.J., Bence, J.R., Eggold, B.T., Makauskas, D. and Clapp, D.F. (2005) Yellow perch dynamics in southwestern Lake Michigan during 1986–2002. *North American Journal of Fisheries Management* **25**, 1130–1152.

Wilen, J.E., Smith, M.D., Lockwood, D. and Botsford, L.W. (2002) Avoiding surprises: incorporating fisherman behavior into management models. *Bulletin of Marine Science* **70**, 553–575.

Winemiller, K.O. (2005) Life history strategies, population regulation, and implications for fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 872–885.

Winemiller, K.O. and Rose, K.A. (1992) Patterns of life-history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 2196–2218.

Wootton, R.J. (1984) Introduction: strategies and tactics in fish reproduction. In: *Fish Reproduction: Strategies and Tactics* (eds G.W. Poots and R.J. Wootton). Academic Press, London, pp. 1–12.

Worm, B., Hilborn, R., Baum, J.K. *et al.* (2009) Rebuilding global fisheries. *Science* **325**, 578–585.

Appendix

Table A1 Model equations.

	Equation	Description
Individual-angler utility		
1	$U_{ij} = U_{0j} + U_{cj} + U_{sj} + U_{xj} + U_{aj} + U_{rj} + U_{oj}$	Conditional indirect utility gained by an angler of type j from choosing to fish (where U_{0j} is the basic utility gained from fishing, U_{cj} is the PWU of daily catch, U_{sj} is the PWU of average size of fish caught annually, U_{xj} is the PWU of maximum size of fish caught annually, U_{aj} is the PWU of angler crowding, U_{rj} is the PWU of minimum-size limit, and U_{oj} is the PWU of annual licence cost)
Angler-effort dynamics		
2a	$p_{tj} = \exp(\hat{U}_{tj})/[\exp(U_{n}) + \exp(\hat{U}_{tj})]$	Probability an angler of type j chooses to fish, over the alternative to not fish (where $\hat{U}_{tj}$ applies to the previous year and U_{n} is the utility gained from not fishing)
2b	$p_{Fj} = (1 - \varphi)p_{tj} + \varphi\hat{p}_{Fj}$	Realized probability an angler of type j chooses to fish (where $\hat{p}_{Fj}$ applies to the previous year)
2c	$D_j = p_{Fj}D_{max}$	Number of days an angler of type j chooses to fish during a year
2d	$A_{Lj} = \rho_j A_L$	Density of licensed anglers of type j
2e	$E_j = D_j A_{Lj}\Psi$	Total annual realized fishing effort density by anglers of type j
2f	$e_{jt} = \begin{cases} E_j/S_F & \text{if } t \le S_F \\ 0 & \text{if } t > S_F \end{cases}$	Instantaneous fishing effort density at time t by anglers of type j
Age-structured fish population		
3a	$N_{total} = \sum_{a=0}^{a_{max}} N_a$	Total fish population density
3b	$B_{total} = \sum_{a=0}^{a_{max}} N_a W_a$	Total fish biomass density
Growth		
4a	$h = h_{max}/[1 + B_{total}/B_{1/2}]$	Maximum annual growth of a fish dependent on the total fish biomass density at the beginning of the year

Table A1 Continued.

	Equation	Description
4b	$p_a = \begin{cases} 1 - \frac{G}{3+G}(1 + L_{a0}/h) & \text{if } a \geq a_m - 1 \\ 1 & \text{if } a < a_m - 1 \end{cases}$	Proportion of the growing season during which a fish of age a allocates energy to growth
4c	$g_{at} = \begin{cases} h/S_G & \text{if } t \leq p_a S_G \\ 0 & \text{if } t > p_a S_G \end{cases}$	Instantaneous growth rate in length of a fish of age a at time t
4d	$L_{at} = L_{a0} + g_{at}t$	Length of a fish of age a at time t
4e	$W_{at} = wL_{at}^{l}$	Mass of a fish of age a at time t
Reproduction		
5a	$R_a = \begin{cases} \delta W_{at_R} GSI / W_e & \text{if } a \geq a_m \\ 0 & \text{if } a < a_m \end{cases}$	Annual fecundity of a female of age a given their mass at time t_R
5b	$b = \Phi \sum_{a=a_m}^{a_{max}} R_a N_a$	Annual population fecundity density (pulsed at the beginning of the year)
5c	Beverton–Holt: $s_0 = \alpha_{BH}/(1 + \beta_{BH}b)$ Ricker: $s_0 = \alpha_R \exp(-\beta_R b)$	Survival probability from spawning to post-hatch of fish of age 0 (applied at the beginning of the year)
5d	$N_0 = s_0 b$	Density of fish of age 0 at the beginning of the year
Mortality		
6a	$v_{ajt} = [1 + \exp(-y(L_{at} - L_{50j}))]^{-1}$	Proportion of fish of age a that are vulnerable to capture by anglers of type j at time t
6b	$L_{50} = z_j L_{max} + L_{shift}$	Size at 50% vulnerability to capture
6c	$c_{ajt} = q_j e_{jt} v_{ajt}$	Instantaneous per capita catch rate of fish of age a by anglers of type j at time t
6d	$H_{ajt} = \begin{cases} 1 & \text{if } L_{at} \geq MSL \\ f_{nj} & \text{if } L_{at} < MSL \end{cases}$	Proportion of fish of age a that are harvestable by anglers of type j at time t
6e	$C_{jt} = \sum_{a=0}^{a_{max}} c_{ajt} N_a H_{ajt}$	Instantaneous catch rate of fish that are harvestable by anglers of type j at time t
6f	$C_{Hjt} = \min(C_{jt}, c_{maxj} e_{jt} \Psi)$	Instantaneous harvest rate by anglers of type j at time t
6g	$f_{Hjt} = C_{Hjt}/C_{jt} + f_{hj}(C_{jt} - C_{Hjt})/C_{jt}$	Proportion of harvestable fish killed by anglers of type j at time t
6h	$m_{fajt} = f_{Hjt} c_{ajt} H_{ajt} + f_{hj} c_{ajt}(1 - H_{ajt})$	Instantaneous per capita fishing mortality rate of fish of age a from anglers of type j at time t
6i	$d_{at} = m_{na} + \sum_j m_{fajt}$	Instantaneous per capita mortality rate of fish of age a at time t
6j	$dN_a/dt = -d_{at} N_a$	Instantaneous rate of change in the density of fish of age a at time t
Response variables		
7a	$SPR = b_F/b_U$	Spawning-potential ratio (= annual population fecundity density b_F under fishing relative to annual population fecundity density b_U under unfished conditions)
7b	$U_{TU} = \sum_j U_{ij} D_j A_{Lj}$	Annual total utility
7c	$P_{Rj} = \frac{E_j / \sum_i E_i}{\rho_j}$	Relative participation of anglers of type j in a mixed angler population

Variables are listed in Table A2. Parameter values and their sources for the fish life-history types studied here are listed in Table S1. Equations for part-worth-utility (PWU) functions are given in Table S2. Parameters describing angler types and PWU functions are specified in Table S3.

Table A2 Model variables. Bioeconomic model equations are listed in Table A1, and parameters for life-history types are listed in Table S1. Angler types and their dynamics are specified in Tables S2 and S3.

Symbol	Description (unit, where applicable)	Value or range
Index variables		
t	Time within the year (years)	0.0–1.0
a	Age class (years)	0–a_{max}
j	Angler type	generic; consumptive; trophy

Table A2 Continued.

Symbol	Description (unit, where applicable)	Value or range
Angling regulations		
MSL	Minimum-size limit (cm)	0–L_{max}
A_L	Licence density (= number of licences issued for a given area) (ha^{-1})	0–1
Age-structured fish population		
N_a	Density of fish of age *a* (ha^{-1})	0–∞
L_{a0}	Length of fish of age *a* at the beginning of a year (cm)	0–L_{max}

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Parameters, with their units, values, and sources, for the five modelled fish life-history types (LHTs).

Table S2. Equations for angler part-worth-utility (PWU) functions, standardized for fish life-history type.

Table S3. Parameters, with their units and values, for the three modelled angler types (generic, consumptive, and trophy anglers).

Table S4. LHT-dependent baseline values for fishery attributes used in part-worth-utility functions.

Table S5. Sensitivities of predicted optimal minimum-size limits to changes (±10%) in life-history parameters of different fish life-history types exploited by homogeneous populations of generic, consumptive, or trophy anglers.

Table S6. Sensitivities of predicted optimal license densities to changes (±10%) in life-history parameters of different fish life-history types exploited by homogeneous populations of generic, consumptive, and trophy anglers.

Table S7. Predicted spawning-potential ratios (SPRs) under optimal minimum-size limits and license densities resulting from changes (±10%) in life-history parameters of different fish life-history types exploited by homogeneous populations of generic, consumptive, and trophy anglers.

Data S1. Parameterization of density-dependent somatic growth and stock-recruitment relationships.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

Supplementary material

Parameters for life-history types

Table S1. Parameters, with their units, values, and sources, for the five modelled fish life-history types (LHTs). Sources are indicated by numbers and listed below. Where a single parameter value is given, it is used for all five LHTs. Bioeconomic model equations are listed in Table A1. Angler types and their dynamics are specified in Tables S2 and S3.

Symbol	Description (unit, where applicable)	Equation	Value or range for fish life-history types (source, where applicable)				
			Perch	Brown trout	Pikeperch	Pike	Bull trout
Growth							
a_{max}	Maximum age of a fish (y)		20 (7)	15 (3)	16 (4)	15 (2)	20 (12)
L_{max}	Maximum size a fish can attain at maximum age ($a = a_{max}$) in an environment free of intraspecific competition ($B_{total} = 0$) (cm)	6b	38.5	51.5	103	117	98
h_{max}	Maximum annual growth increment (cm)	4a	6.3 (†)	9.4 (†)	14.2 (†)	24.0 (†)	10.6 (†)
$B_{1/2}$	Total fish biomass density at which the growth increment is halved (kg·ha^{-1})	4a	344.8 (†)	256.4 (†)	144.9 (†)	100.0 (†)	26.3 (†)
G	Annual reproductive investment	4b	0.47 (†)	0.51 (†)	0.36 (†)	0.58 (†)	0.29 (†)
a_m	Age at first spawning (y)	4b, 5a	3 (7)	3 (18) (*)	4 (16)	2 (13)	7 (11) (*)
L_0	Length of fish at hatch (cm)	4b	0.6 (24)	1.5 (14)	0.5 (21)	0.8 (5)	1.5 (6)
S_G	Annual duration of the growing season (y)	4c			1.0		

w	Scaling constant for length-mass relationship ($g \cdot cm^{-l}$)	4e	0.0104 (1)	0.0107 (4)	0.0058 (4)	0.0048 (23)	0.0085 (11)
l	Allometric exponent for length-mass relationship	4e	3.14 (1)	3.003 (4)	3.148 (4)	3.059 (23)	3.059 (11)
Reproduction							
t_R	Relative time in the year when spawning occurs (spring vs. fall)	5a	0.00 = Spring (7)	-0.17 = Fall (14)	0.00 = Spring (16)	0.00 = Spring (12)	-0.17 = Fall (12)
GSI	Gonadosomatic index (= gonadic mass/somatic mass)	5a	0.21 (19)	0.18 (18)	0.10 (21)	0.17 (8)	0.15 (9)
W_e	Average egg mass (g)	5a	0.0024 (19)	0.0700 (3)	0.0005 (20)	0.0050 (8)	0.0600 (9)
δ	Proportion of eggs that hatch	5a			0.75 (13, 21)		
Φ	Proportion of female fish in the spawning population	5b			0.5		
α	Maximum proportion of offspring surviving from spawning to post-hatch (Ricker, R; Beverton-Holt, BH)	5c	Ricker $\alpha_R = 3.25 \cdot 10^{-3}$ (‡)	Ricker $\alpha_R = 3.26 \cdot 10^{-2}$ (‡)	Ricker $\alpha_R = 2.32 \cdot 10^{-5}$ (‡)	Ricker $\alpha_R = 1.71 \cdot 10^{-4}$ (‡)	Beverton-Holt $\alpha_{BH} = 3.32 \cdot 10^{-3}$ (‡)
β	Inverse population density at which offspring survival is divided by $e = 2.71$ (Ricker, R) or by 2 (Beverton-Holt, BH) (ha)	5c	Ricker $\beta_R = 1.99 \cdot 10^{-6}$ (‡)	Ricker $\beta_R = 7.46 \cdot 10^{-5}$ (‡)	Ricker $\beta_R = 3.47 \cdot 10^{-7}$ (‡)	Ricker $\beta_R = 6.87 \cdot 10^{-6}$ (‡)	Beverton-Holt $\beta_{BH} = 1.34 \cdot 10^{-3}$ (‡)

Mortality

m_{na}	Instantaneous natural mortality rate of fish of age a (y^{-1})	6i	0.00 if $a = 0$ 0.41 if $a > 0$ (15)	0.00 if $a = 0$ 0.56 if $a > 0$ (3)	0.00 if $a = 0$ 0.26 if $a > 0$ (17)	0.00 if $a = 0$ 0.46 if $a > 0$ (22)	0.00 if $a = 0$ 0.20 if $a > 0$ (10)
a_{max}	Maximum age of fish (y)		20 (7)	15 (3)	16 (4)	15 (2)	20 (12)

Sources: (1) Buijse et al. (1992), (2) Craig and Kipling (1983), (3) Crisp (1994), (4) Froese and Pauly (2010), (5) Frost and Kipling (1967), (6) Gould (1987), (7) Heibo et al.(2005), (8) Hubenova et al. (2007), (9) unpublished data (F. Johnston), (10) Johnston et al. (2007), (11) Johnston and Post (2009), (12) Joynt and Sullivan (2003), (13) Kipling and Frost (1970), (14) Klemetsen et al. (2003), (15) Le Cren et al. (1977), (16) Lehtonen et al. (1996), (17) Lind (1977), (18) Lobón-Cerviá et al. (1986), (19) Øxnevad et al. (2002), (20) Rónyai (2007) (21) Schlumberger and Proteau (1996), (22) Treasurer et al. (1992), (23) Willis (1989), (24) Ylikarjula et al. (2002).

Species names: European perch (*Perca fluviatilis*, Percidae), brown trout (*Salmo trutta*, Salmonidae), pikeperch (*Sander lucioperca*, Percidae), northern pike (*Esox lucius*, Esocidae), and bull trout (*Salvelinus confluentus*, Salmonidae).

* This specifies a first-time-spawner's age when the eggs hatch; however these fish matured and spawned during the previous fall.

† For sources and details, see section "Parameterization of density-dependent somatic growth" below.

‡ For sources and details, see section "Parameterization of stock-recruitment relationships" below.

Equations for part-worth-utility functions

Table S2. Equations for angler part-worth-utility (PWU) functions, standardized for fish life-history type. Parameters are listed in Table S3, and baseline values are listed in Table S4.

	Equation	Description
	Standardized fishery attributes	
S1a	$c_{\mathrm{D}} = C_{\mathrm{Do}} / C_{\mathrm{De}} \Psi - 1$ (*)	Standardized relative daily catch
S1b	$\overline{l} = \overline{L}_{\mathrm{o}} / \overline{L}_{\mathrm{e}} - 1$ (*)	Standardized relative average size of fish caught annually
S1c	$l_{\mathrm{x}} = L_{\mathrm{xo}} / L_{\mathrm{xe}} - 1$ (*)	Standardized relative maximum size of fish caught annually
S1d	$A = \sum_j D_j A_{\mathrm{L}j} \phi / (365 S_{\mathrm{F}})$	Observed average number of anglers fishing in a day (Table A1, equation 2c)
S1e	$r = MSL / L_{\max}$	Standardized minimum-size limit MSL
S1f	$o = O_{\mathrm{o}} - O_{\mathrm{e}}$ (*)	Standardized relative annual license cost
	Part-worth-utility (PWU) functions	
S2a	$U_{cj} = u_{1j} c_{\mathrm{D}} + u_{2j} c_{\mathrm{D}}^2$	PWU of daily catch
S2b	$U_{sj} = u_{3j} \overline{l} + u_{4j}$	PWU of average size of fish caught annually
S2c	$U_{\mathrm{x}j} = \begin{cases} u_{5j} l_{\mathrm{x}}{}^2 & \text{if } l_{\mathrm{x}} \geq 0 \\ -u_{5j} l_{\mathrm{x}}{}^2 & \text{if } l_{\mathrm{x}} < 0 \end{cases}$	PWU of maximum size of fish caught annually
S2d	$U_{aj} = u_{6j} A + u_{7j} A^2 + u_{8j}$	PWU of angler crowding
S2e	$U_{rj} = u_{9j} r + u_{10j} r^2 + u_{11j}$	PWU of minimum-size limit MSL
S2f	$U_{oj} = u_{12j} o$	PWU of annual license cost

* O_{o} is the observed annual fishing license cost, C_{Do} is the observed average daily catch, $\overline{L}_{\mathrm{o}}$ is the observed average size of fish caught annually, and L_{xo} is the observed maximum size of fish caught annually (defined as the 95$^{\mathrm{th}}$ percentile of the size distribution of fish caught annually).

Parameters for angler types

Table S3. Parameters, with their units and values, for the three modelled angler types (generic, consumptive, and trophy anglers). Where a single parameter value is given, it is used for all three angler types. The referenced equations are listed in Table A1 and Table S2.

Symbol	Description (unit, where applicable)	Equation	Value (generic; consumptive; trophy)
	Fishing practices		
y (*)	Steepness of size-dependent vulnerability curve	6a	0.36
z_j (*)	Size as a proportion of $L_{\max}$ used when calculating the size L_{50} at which 50% of the fish are vulnerable to capture	6b	0.18; 0.18; 0.28
L_{shift}	Constant used to when calculating the size L_{50} (cm)	6b	10
q_j	Catchability reflecting skill level (ha h^{-1})	6c	0.011; 0.020; 0.025
$c_{\max j}$	Desired average number of fish an angler will harvest daily	6f	2; ∞; 0.5
$f_{\text{h}j}$	Proportion of fish dying from hooking mortality	6g, 6h	0.05
$f_{\text{n}j}$	Proportion of fish below the minimum-size limit MSL harvested illegally	6d	0.05
	Angler population		
ρ_j	Proportion of angler population composed of anglers of type j	2d, 7c	non-mixed: 1.0 for one j; 0.0 for the others mixed-0: 0.4; 0.3; 0.3 mixed-1: 0.70; 0.15; 0.15 mixed-2: 0.15; 0.70; 0.15

			mixed-3: 0.15; 0.15; 0.70
	Angler-effort dynamics		
U_{n}	Conditional indirect utility gained by an angler from choosing not to fish	2a	0
φ	Persistence of fishing behaviour (= relative influence of last year's realized fishing probability on the current year's realized fishing probability)	2b	0.5
$D_{\max}$	Maximum number of days that an angler would fish per year irrespective of fishing quality	2c	40
Ψ	Average time an angler will fish in a day (h)	2e, 6f, S1a	4
ϕ	Lake area (ha)	S1d	100
S_{F}	Annual duration of fishing season (y)	2f, S1d	9/12
	Part-worth-utility functions		
U_{0j}	Basic utility gained by an angler of type j from choosing to fish	1	-0.405; 0.000; 0.405
u_{1j}	PWU linear coefficient	S2a	0.968; 1.318; 0.825
u_{2j}	PWU quadratic coefficient	S2a	-0.121; -0.220; -0.206
u_{3j}	PWU linear coefficient	S2b	2.476; 3.389; 4.394
u_{4j}	PWU constant coefficient	S2b	0.000; 0.000; -0.220 (†)
u_{5j}	PWU quadratic coefficient	S2c	9.414; 6.878; 12.207
u_{6j}	PWU linear coefficient	S2d	0.244; 0.149; 0.136
u_{7j}	PWU quadratic coefficient	S2d	-0.031; -0.025; -0.034

u_{8j}	PWU constant coefficient	S2d	0.610; 0.396; 0.712
u_{9j}	PWU linear coefficient	S2e	2.321; 3.766; 2.534
u_{10j}	PWU quadratic coefficient	S2e	-3.869; -9.414; -2.534
u_{11j}	PWU constant coefficient	S2e	0.271; 0.471; -0.228
u_{12j}	PWU linear coefficient	S2f	-0.015; -0.011; -0.008

* Predicted vulnerability values are in fairly good agreement with empirical information for similar species, e.g.:, yellow perch at 27 cm is 100% vulnerable (Wilberg et al., 2005), compared with 95% for European perch in our model; rainbow trout at 30-35 cm is 100% vulnerable (van Poorten and Post, 2005), compared with 96%-99% for brown trout in our model; pike at 55 cm is 100% vulnerable (Arlinghaus et al., 2009), compared with 100% for pike in our model; bull trout at 35 cm is 100% vulnerable (Paul et al., 2003), compared with 90% for bull trout in our model.

† The intercept u_{4j}, from the PWU function of average size of fish caught annually, for trophy anglers represents a 5% increase of the average-size baseline value relative to that of generic and consumptive anglers. This reflects the fact that more specialized anglers have been found to use a larger minimum length when defining quality-sized fish (Hahn, 1991).

Table S4. LHT-dependent baseline values for fishery attributes used in part-worth-utility functions. These baseline values specify the fishery-attribute level at which the corresponding part-worth utility gained by anglers equals zero. Where baseline values do not differ among LHT, only one value, or set of values, is given. Where baseline values differ among angler types, three values are given for generic, consumptive, and trophy anglers, respectively. Where applicable, values reported in the literature for similar or closely related species are provided in square brackets for comparative purposes. Sources are indicated by numbers and listed below.

Fishery attribute (units) (relevant table and equation)	Symbol	Life-history type [literature values (source)]				
		Perch	Brown trout	Pikeperch	Pike	Bull trout
Catch rate (h^{-1}) (Table S2, equation 8a)	C_{De}	1.90 [yellow perch 0.05-5.0 (4), European perch 1.2-4.3 (2)]	0.95 [Spanish rivers 1.3-6.9 (1), UK upland lakes 0.46-1.44 (7)]	0.41 [0.11-0.69 (2)]	0.12 [0.10-0.38 (6)]	0.06 [0.11-0.34 (5)]
Average size (cm) (Table S2, equation 8b)	$\overline{L}_e$	20 [yellow perch 21 (3)]	26 [anadromous 41 (3), UK lakes 25-28 (7)]	46 [walleye 42 (3)]	52 [58 (3)]	44 [dolly varden 41 (3)]
Maximum size (cm) (Table S2, equation 8c)	L_{xe}	26 [yellow perch 29 (3)]	33 [anadromous 54 (3)]	62 [walleye 59 (3)]	69 [80 (3)]	58 [dolly varden 56 (3)]
Crowding (d^{-1})				10; 8; 7		
Minimum-size limit (as a proportion of L_{max})				0.7; 0.5; 0.9		
Cost (€) (Table S2, equation 8f)	O_e			75		

Sources: (1) Almodóvar and Nicola (1998), (2) unpublished data (M. Dorow and R. Arlinghaus), (3) Gabelhouse (1984), (4) Isermann et al. (2005), (5) Paul et al. (2003), (6) Pierce et al. (1995), (7) Swales and Fish (1986).
Species names: Yellow perch (*Perca flavescens*, Percidae), walleye (*Sander vitreus*, Percidae), dolly varden (*Salvelinus malma*, Salmonidae).

Parameterization of density-dependent somatic growth

To parameterize the density-dependent growth relationships (Table A1, equation 4a), empirical length-at-age data and biomass-density data from various studies were used to estimate the maximum annual growth increment $h_{\max}$, the total fish biomass density $B_{1/2}$ at which the growth increment is halved, and the annual reproductive investment G, by minimizing the corresponding sums of squares (using the Solver® function of Microsoft® Office Excel 2003).

The empirical studies from which this data was extracted are as follows: pike (Kipling and Frost, 1970, Kipling, 1983a, Treasurer et al., 1992, Pierce and Tomcko, 2003, Pierce et al., 2003, Pierce and Tomcko, 2005); pikeperch (Buijse et al., 1992) unpublished data, H. Winkler); perch (Le Cren, 1958, Craig et al., 1979, Treasurer et al., 1992, Treasurer, 1993); brown trout (Jenkins et al., 1999, Nicola and Almodóvar, 2002, Almodóvar and Nicola, 2004); bull trout (Johnston and Post, 2009) unpublished data, F. Johnston).

The estimated maximum annual growth increments $h_{\max}$ are in general agreement with literature values: 24.0 cm for pike in our model, compared with 27.1 cm (Arlinghaus et al., 2009); 10 cm for pikeperch in our model, compared with 9-12 cm (Biró, 1985); 5.5 cm for perch in our model, compared with 5-15 cm (Heibo et al., 2005); 8.4 cm for brown trout in our model, compared with 8-11 cm (Jenkins et al., 1999); 7.7 cm for bull trout in our model, compared with 10 cm (Paul et al., 2003).

Parameterization of stock-recruitment relationships

To parameterize the Ricker (R) and Beverton-Holt (BH) stock-recruitment relationships (Table A1, equation 5c), empirical length-at-age and biomass-density data from various studies were used to estimate the maximum proportion of offspring surviving from spawning to post-hatch (α_{R} or α_{BH}) and the inverse population density at which offspring survival is divided by $e = 2.71$ (β_{R}) or 2 (β_{BH}).

For pike, egg density was determined using a relative fecundity relationship (Craig and Kipling, 1983), adult biomass (Kipling, 1983b), and corresponding area (1480 ha, Le Cren et al., 1977), with the density of pike aged 1 year back-calculated from natural mortality (Kipling and Frost, 1970) and the abundance of pike aged 2 years (Le Cren et al., 1977). For

pikeperch, egg density was determined using the relative fecundity relationship (Schlumberger and Proteau, 1996), adult biomass, and corresponding area (19700 ha, unpublished data, H. Winkler), with adult biomass back-calculated from commercial catch (Lehtonen et al., 1996) and exploitation rate (Gröger et al., 2007), and the density of pikeperch aged 1 year back-calculated from natural mortality information (Lind, 1977) and the abundance of pikeperch aged 2 years (Gröger et al., 2007). For perch, egg density was determined using a relative fecundity relationship (Treasurer, 1981), adult biomass (Craig et al., 1979), and corresponding area (1480 ha, Le Cren et al., 1977), with the density of perch aged 1 year back-calculated from natural mortality information (Le Cren et al., 1977) and the abundance of perch aged 2 years (Le Cren et al., 1977). For brown trout, a stock-recruitment relationship for a migratory brown-trout population from England (Elliott, 1985) was scaled so that egg density and the density of brown trout aged 1 year (May/June) in the spawning stream result in a population density in line with literature values: the chosen target fish density of 300 ha^{-1} is roughly based on the density of 229 ha^{-1} observed for a British lake (Swales, 1986), although this is low compared with the density of 560-4900 ha^{-1} observed for more productive rivers in Spain (Nicola and Almodóvar, 2002). For bull trout, the stock-recruitment relationship reported by Post et al. (2003) was scaled to account for the corresponding lake area (646 ha, (Johnston et al., 2007).

The population densities predicted using these estimates under unexploited conditions generally fall within the ranges reported in the literature (although pikeperch are likely more abundant in our model than in average natural settings, whereas the densities of perch and bull trout in our model are on the low side of the reported empirical ranges): for perch, 779 ha^{-1} in our model, compared with 675-4189 ha^{-1} (Craig et al., 1979); for brown trout, 300 ha^{-1} in our model, compared with 229 ha^{-1} in a British lake (Swales, 1986) and 560-4900 ha^{-1} in more productive rivers in Spain (Nicola and Almodóvar, 2002); for pikeperch aged 3 years and older, 56 ha^{-1} in our model, compared with 26-42 ha^{-1} (Lehtonen, 1979); for pike, 23 ha^{-1} in our model, compared with 11.0-55.1 ha^{-1} (Pierce et al., 1995); for bull trout, 12 ha^{-1} in our model, and for adult bull trout, 4.4 ha^{-1} in our model, compared with, respectively, 12-38 ha^{-1} (Parker et al., 2007) and less than 2.7 ha^{-1} (Johnston et al., 2011).

Sensitivity analyses

Table S5. Sensitivities of predicted optimal minimum-size limits to changes (±10%) in life-history parameters of different fish life-history types exploited by homogeneous populations of generic, consumptive, or trophy anglers. The table shows the relative changes in optimal minimum-size limits compared with those predicted by the original model. Changes greater than 10% (highlighted by a grey background) indicate a particular sensitivity to changes in the considered life-history parameter.

Life-history type	Angler type	Parameter change	Life-history parameter									
			h_{max}	$B_{1/2}$	G	W_e	GSI	α	β	m_{na}	a_m	a_{max}
Perch	Generic	+10%	2.6%	0.0%	0.0%	0.0%	0.0%	0.0%	2.6%	0.0%	0.0%	0.0%
		-10%	0.0%	2.6%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
	Consumptive	+10%	0.0%	-2.6%	0.0%	0.0%	0.0%	-2.6%	-2.6%	0.0%	0.0%	0.0%
		-10%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	-2.6%	-2.6%	-2.6%	0.0%
	Trophy	+10%	5.2%	0.0%	5.2%	0.0%	0.0%	0.0%	0.0%	2.6%	5.2%	0.0%
		-10%	2.6%	0.0%	-5.2%	0.0%	0.0%	0.0%	2.6%	5.2%	2.6%	0.0%
Brown trout	Generic	+10%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	-1.9%	-1.9%	0.0%
		-10%	-3.9%	0.0%	0.0%	0.0%	0.0%	-1.9%	0.0%	-3.9%	-1.9%	0.0%
	Consumptive	+10%	-3.9%	0.0%	-1.9%	0.0%	0.0%	0.0%	0.0%	0.0%	-5.8%	0.0%
		-10%	-3.9%	0.0%	1.9%	0.0%	0.0%	0.0%	0.0%	0.0%	-3.9%	0.0%
	Trophy	+10%	7.8%	0.0%	3.9%	1.9%	-1.9%	3.9%	-1.9%	5.8%	11.7%	0.0%
		-10%	7.8%	-1.9%	-1.9%	0.0%	0.0%	-1.9%	0.0%	3.9%	1.9%	1.9%
Pikeperch	Generic	+10%	0.0%	-1.0%	2.9%	0.0%	0.0%	-1.0%	0.0%	0.0%	2.9%	0.0%
		-10%	-1.0%	1.0%	1.0%	0.0%	0.0%	0.0%	-1.0%	-1.0%	-1.0%	0.0%
	Consumptive	+10%	-1.0%	-1.0%	-1.9%	0.0%	-1.0%	-1.0%	0.0%	0.0%	1.0%	-1.0%
		-10%	-1.0%	0.0%	-2.9%	-1.0%	-1.0%	0.0%	-1.0%	-1.0%	-1.9%	-1.0%
	Trophy	+10%	5.8%	-1.0%	-2.9%	0.0%	0.0%	-1.0%	1.9%	2.9%	0.0%	4.9%

		-10%	-1.9%	2.9%	2.9%	0.0%	0.0%	1.9%	-1.0%	1.9%	2.9%	0.0%
Pike	Generic	+10%	6.8%	0.0%	7.7%	0.0%	0.0%	0.0%	0.9%	0.9%	11.1%	0.0%
		-10%	-4.3%	0.9%	2.6%	10.3%	0.0%	0.9%	0.0%	9.4%	10.3%	0.0%
	Consumptive	+10%	4.3%	0.0%	-1.7%	0.0%	0.0%	0.0%	-6.8%	-6.8%	3.4%	0.0%
		-10%	1.7%	0.9%	1.7%	0.0%	0.0%	0.0%	0.0%	0.9%	-1.7%	0.0%
	Trophy	+10%	-4.3%	-0.9%	-5.1%	0.0%	0.0%	-0.9%	0.9%	-9.4%	-9.4%	0.0%
		-10%	-10.3%	0.9%	6.0%	0.0%	0.0%	0.9%	-0.9%	-5.1%	-1.7%	0.0%
Bull trout	Generic	+10%	4.1%	-1.0%	-3.1%	0.0%	0.0%	-1.0%	0.0%	2.1%	-45.4%	0.0%
		-10%	-5.2%	1.0%	2.1%	0.0%	0.0%	1.0%	0.0%	-1.0%	-1.0%	0.0%
	Consumptive	+10%	-44.3%	1.0%	1.0%	1.0%	0.0%	0.0%	0.0%	-24.7%	-11.3%	0.0%
		-10%	-10.3%	0.0%	0.0%	-1.0%	-1.0%	-1.0%	-1.0%	20.6%	1.0%	0.0%
	Trophy	+10%	6.2%	-2.1%	-5.2%	1.0%	1.0%	-1.0%	1.0%	-2.1%	-50.5%	0.0%
		-10%	-4.1%	1.0%	4.1%	-1.0%	1.0%	1.0%	1.0%	-4.1%	-1.0%	0.0%

Table S6. Sensitivities of predicted optimal license densities to changes (±10%) in life-history parameters of different fish life-history types exploited by homogeneous populations of generic, consumptive, and trophy anglers. The table shows the relative changes in optimal license densities compared with those predicted by the original model. Changes greater than 10% (highlighted by a grey background) indicate a particular sensitivity to changes in the considered life-history parameter.

Life-history prototype	Angler type	Parameter change	Life-history parameter									
			h_{max}	$B_{1/2}$	G	W_e	GSI	α	β	$m_{n\alpha}$	a_m	a_{max}
Perch	Generic	+10%	-3.4%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	-1.7%	1.7%	0.0%
		-10%	-3.4%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	-1.7%	-1.7%	0.0%
	Consumptive	+10%	18.4%	0.0%	-2.6%	0.0%	0.0%	2.6%	-2.6%	-10.5%	-13.2%	0.0%
		-10%	10.5%	-2.6%	2.6%	-2.6%	0.0%	-2.6%	0.0%	2.6%	5.3%	0.0%
	Trophy	+10%	11.4%	4.5%	4.5%	-4.5%	4.5%	4.5%	-4.5%	6.8%	9.1%	0.0%
		-10%	2.3%	-2.3%	-2.3%	4.5%	-2.3%	-2.3%	4.5%	6.8%	4.5%	0.0%
Brown trout	Generic	+10%	3.7%	0.0%	-1.9%	0.0%	-1.9%	1.9%	-1.9%	-3.7%	-3.7%	0.0%
		-10%	-11.1%	0.0%	0.0%	-1.9%	0.0%	-1.9%	0.0%	-7.4%	-1.9%	0.0%
	Consumptive	+10%	-2.1%	8.3%	6.3%	2.1%	0.0%	8.3%	4.2%	0.0%	-52.1%	0.0%
		-10%	-4.2%	0.0%	10.4%	0.0%	0.0%	4.2%	4.2%	8.3%	-4.2%	0.0%
	Trophy	+10%	16.7%	0.0%	4.8%	-4.8%	0.0%	-2.4%	-2.4%	9.5%	16.7%	0.0%
		-10%	4.8%	-2.4%	-2.4%	-4.8%	-7.1%	0.0%	0.0%	14.3%	7.1%	-2.4%
Pikeperch	Generic	+10%	-3.7%	0.0%	-3.7%	-1.9%	3.7%	-1.9%	-1.9%	-1.9%	1.9%	0.0%
		-10%	1.9%	5.6%	1.9%	3.7%	-1.9%	0.0%	-3.7%	-1.9%	0.0%	0.0%
	Consumptive	+10%	-2.3%	-4.7%	-9.3%	-2.3%	-14.0%	-2.3%	-9.3%	-9.3%	-11.6%	-9.3%
		-10%	-14.0%	2.3%	-2.3%	-16.3%	-7.0%	-7.0%	-4.7%	0.0%	-2.3%	-9.3%
	Trophy	+10%	-6.3%	0.0%	-8.3%	0.0%	0.0%	-2.1%	-6.3%	-8.3%	-4.2%	-16.7%
		-10%	-10.4%	-2.1%	-6.3%	0.0%	0.0%	-6.3%	0.0%	-10.4%	-12.5%	-6.3%

Pike	Generic	+10%	7.5%	3.8%	7.5%	0.0%	0.0%	5.7%	1.9%	-3.8%	7.5%	0.0%
		-10%	0.0%	0.0%	-3.8%	1.9%	0.0%	3.8%	0.0%	9.4%	7.5%	0.0%
	Consumptive	+10%	2.4%	-2.4%	-14.3%	2.4%	-7.1%	-2.4%	-21.4%	-31.0%	-9.5%	0.0%
		-10%	-9.5%	11.9%	-7.1%	-7.1%	4.8%	-19.0%	-4.8%	2.4%	-14.3%	0.0%
	Trophy	+10%	25.0%	0.0%	5.0%	0.0%	0.0%	-2.5%	-2.5%	17.5%	20.0%	0.0%
		-10%	10.0%	-2.5%	-7.5%	0.0%	0.0%	-2.5%	2.5%	15.0%	12.5%	0.0%
Bull trout	Generic	+10%	-5.4%	3.6%	1.8%	1.8%	0.0%	1.8%	0.0%	-8.9%	25.0%	1.8%
		-10%	-8.9%	-1.8%	-14.3%	0.0%	1.8%	0.0%	1.8%	-12.5%	0.0%	0.0%
	Consumptive	+10%	690.9%	9.1%	9.1%	9.1%	0.0%	0.0%	0.0%	-18.2%	700.0%	0.0%
		-10%	-18.2%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	172.7%	9.1%	0.0%
	Trophy	+10%	-4.5%	0.0%	0.0%	4.5%	2.3%	4.5%	2.3%	9.1%	77.3%	0.0%
		-10%	-9.1%	-2.3%	0.0%	-4.5%	6.8%	0.0%	6.8%	4.5%	2.3%	0.0%

Table S7. Predicted spawning-potential ratios (*SPR* s) under optimal minimum-size limits and license densities resulting from changes (±10%) in life-history parameters of different fish life-history types exploited by homogeneous populations of generic, consumptive, and trophy anglers. *SPR* values below 0.35 (highlighted by a grey background) indicate a risk of recruitment overfishing.

Life-history type	Angler type	Parameter change	Life-history parameter									
			h_{max}	$B_{1/2}$	G	W_e	GSI	α	β	$m_{n\alpha}$	a_m	a_{max}
Perch	Generic	+10%	0.87	0.87	0.88	0.87	0.87	0.88	0.86	0.88	0.85	0.87
		-10%	0.88	0.87	0.86	0.87	0.87	0.86	0.88	0.87	0.88	0.87
	Consumptive	+10%	0.41	0.48	0.50	0.50	0.47	0.49	0.49	0.51	0.32	0.48
		-10%	0.50	0.48	0.47	0.47	0.50	0.47	0.48	0.47	0.57	0.48
	Trophy	+10%	0.91	0.93	0.93	0.93	0.93	0.93	0.93	0.93	0.91	0.93
		-10%	0.94	0.93	0.92	0.93	0.93	0.93	0.93	0.92	0.93	0.93
Brown trout	Generic	+10%	0.67	0.67	0.67	0.68	0.66	0.69	0.66	0.65	0.57	0.67
		-10%	0.68	0.67	0.67	0.66	0.68	0.64	0.69	0.71	0.73	0.67
	Consumptive	+10%	0.44	0.59	0.58	0.61	0.58	0.60	0.59	0.60	0.32	0.60
		-10%	0.58	0.59	0.59	0.58	0.62	0.57	0.59	0.58	0.67	0.60
	Trophy	+10%	0.83	0.86	0.85	0.86	0.85	0.86	0.85	0.83	0.75	0.85
		-10%	0.85	0.86	0.85	0.85	0.87	0.84	0.86	0.84	0.87	0.86
Pikeperch	Generic	+10%	0.62	0.65	0.73	0.67	0.63	0.66	0.65	0.65	0.66	0.64
		-10%	0.67	0.64	0.64	0.63	0.66	0.64	0.65	0.64	0.67	0.65
	Consumptive	+10%	0.47	0.52	0.53	0.54	0.52	0.53	0.54	0.54	0.48	0.52
		-10%	0.57	0.51	0.43	0.52	0.54	0.52	0.51	0.51	0.54	0.53
	Trophy	+10%	0.69	0.68	0.69	0.68	0.66	0.69	0.69	0.69	0.62	0.73
		-10%	0.71	0.68	0.68	0.66	0.68	0.67	0.67	0.71	0.75	0.69
Pike	Generic	+10%	0.69	0.65	0.76	0.68	0.64	0.67	0.66	0.68	0.75	0.66
		-10%	0.61	0.66	0.67	0.76	0.68	0.64	0.65	0.75	0.76	0.66

	Consumptive	+10%	0.54	0.49	0.49	0.49	0.46	0.50	0.39	0.41	0.47	0.47
		-10%	0.55	0.46	0.50	0.46	0.49	0.49	0.49	0.47	0.49	0.47
	Trophy	+10%	0.70	0.76	0.75	0.77	0.74	0.77	0.76	0.69	0.64	0.75
		-10%	0.71	0.76	0.77	0.74	0.77	0.75	0.75	0.72	0.73	0.76
Bull trout	Generic	+10%	0.61	0.59	0.60	0.60	0.59	0.60	0.59	0.64	0.00	0.59
		-10%	0.61	0.59	0.62	0.59	0.60	0.59	0.60	0.63	0.62	0.60
	Consumptive	+10%	0.00	0.25	0.25	0.25	0.26	0.27	0.26	0.21	0.00	0.26
		-10%	0.27	0.25	0.26	0.25	0.25	0.25	0.25	0.46	0.30	0.27
	Trophy	+10%	0.46	0.44	0.44	0.44	0.43	0.44	0.43	0.39	0.00	0.44
		-10%	0.49	0.44	0.43	0.44	0.43	0.43	0.43	0.42	0.48	0.45

Supplementary references

Almodóvar, A., Nicola, G.G. (1998) Assessment of a brown trout *Salmo trutta* population in the River Gallo (central Spain): angling effects and management implications (Salmonidae). *Italian Journal of Zoology* **65,** 539-539.

Almodóvar, A., Nicola, G.G. (2004) Angling impact on conservation of Spanish stream-dwelling brown trout *Salmo trutta*. *Fisheries Management and Ecology* **11,** 173-182.

Arlinghaus, R., Matsumura, S., Dieckmann, U. (2009) Quantifying selection differentials caused by recreational fishing: development of modeling framework and application to reproductive investment in pike (*Esox lucius*). *Evolutionary Applications* **2,** 335-355.

Biró, P. (1985) Dynamics of the pikeperch, *Stizostedion lucioperca* (L.), in Lake Balaton. *Internationale Revue der gesamten Hydrobiologie und Hydrographie* **70,** 471-490.

Buijse, A., Pet, J.S., van Densen, W.L.T., Machiels, M.A.M., Rabbinge, R. (1992) A size- and age-structured simulation model for evaluating management strategies in a multispecies gill net fishery. *Fisheries Research* **13,** 95-117.

Craig, J.F., Kipling, C. (1983) Reproduction effort versus the environment; case-histories of Windermere perch, *Perca fluviatilis* L., and pike, *Esox lucius* L. *Journal of Fish Biology* **22,** 713-727.

Craig, J.F., Kipling, C., Le Cren, E.D., McCormack, J.C. (1979) Estimates of the numbers, biomass and year-class strengths of perch (*Perca fluviatilis* L.) in Windermere from 1967 to 1977 and some comparisons with earlier years. *Journal of Animal Ecology* **48,** 315-325.

Crisp, D.T. (1994) Reproductive investment of female brown trout, *Salmo trutta* L., in a stream and reservoir system in northern England. *Journal of Fish Biology* **44,** 343-349.

Elliott, J.M. (1985) The choice of a stock-recruitment model for migratory trout, *Salmo trutta*, in an English Lake District stream. *Archiv für Hydrobiologie* **104,** 145-168.

Froese, R., Pauly, D. (2010) Fishbase, Version 05/2010. (Eds. R. Froese, D. Pauly), Available from www.fishbase.org.

Frost, W.E., Kipling, C. (1967) A study of reproduction, early life, weight-length relationship and growth of pike, *Esox lucius* L., in Windermere. *Journal of Animal Ecology* **36,** 651-693.

Gabelhouse, D.W., Jr. (1984) A length-categorization system to assess fish stocks. *North American Journal of Fisheries Management* **4,** 273-285.

Gould, W.R. (1987) Features in the early development of bull trout (*Salvelinus confluentus*). *Northwest Science* **61,** 264-268.

Gröger, J.P., Winkler, H., Rountree, R.A. (2007) Population dynamics of pikeperch (*Sander lucioperca*) and its linkage to fishery driven and climatic influences in a southern Baltic lagoon of the Darss-Zingst Bodden Chain. *Fisheries Research* **84,** 189-201.

Hahn, J. (1991) Angler specialization: measurement of a key sociological concept and implications for fisheries management decisions. *American Fisheries Society Symposium* **12,** 380-389.

Heibo, E., Magnhagen, C., Vøllestad, L.A. (2005) Latitudinal variation in life-history traits in Eurasian perch. *Ecology* **86,** 3377-3386.

Hubenova, T., Zaikov, A., Vasileva, P. (2007) Investigation on fecundity, follicles and free embryo size of pond-reared pike (*Esox lucius*) of different age and size. *Aquaculture International* **15,** 235-240.

Isermann, D.A., Willis, D.W., Lucchesi, D.O., Blackwell, B.G. (2005) Seasonal harvest, exploitation, size selectivity, and catch preferences associated with winter yellow perch anglers on South Dakota lakes. *North American Journal of Fisheries Management* **25,** 827-840.

Jenkins, T.M., Jr., Diehl, S., Kratz, K.W., Cooper, S.D. (1999) Effects of population density on individual growth of brown trout in streams. *Ecology* **80,** 941-956.

Johnston, F.D., Arlinghaus, R., Stelfox, J., Post, J.R. (2011) Decline in angler use despite increased catch rates:anglers' response to the implementation of a total catch-and-release regulation. *Fisheries Research* **110,** 189-197.

Johnston, F.D., Post, J.R. (2009) Density-dependent life-history compensation of an iteroparous salmonid. *Ecological Applications* **19,** 449-467.

Johnston, F.D., Post, J.R., Mushens, C.J., Stelfox, J.D., Paul, A.J., Lajeunesse, B. (2007) The demography of recovery of an overexploited bull trout, *Salvelinus confluentus*, population. *Canadian Journal of Fisheries and Aquatic Sciences* **64,** 113-126.

Joynt, A., Sullivan, M.G. (2003) *Fish of Alberta*, Lone Pine Publishing, Edmonton, AB, Canada.

Kipling, C. (1983a) Changes in the growth of pike (*Esox lucius*) in Windermere. *Journal of Animal Ecology* **52,** 647-657.

Kipling, C. (1983b) Changes in the population of pike (*Esox lucius*) in Windermere from 1944 to 1981. *Journal of Animal Ecology* **52,** 989-999.

Kipling, C., Frost, W.E. (1970) A study of mortality, population numbers, year class strengths, production and food consumption of pike, *Esox lucius* L., in Windermere from 1944 to 1962. *Journal of Animal Ecology* **39,** 115-157.

Klemetsen, A., Amundsen, P.A., Dempson, J.B.*, et al.* (2003) Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater Fish* **12,** 1-59.

Le Cren, E.D. (1958) Observations on the growth of perch (*Perca fluviatilis* L.) over twenty-two years with special reference to the effects of temperature and changes in population density. *Journal of Animal Ecology* **27,** 287-334.

Le Cren, E.D., Kipling, C., McCormack, J.C. (1977) A study of the numbers, biomass and year-class strengths of perch (*Perca fluviatilis* L.) in Windermere from 1941 to 1966. *Journal of Animal Ecology* **46,** 281-207.

Lehtonen, H. (1979) Stock assessment of pike-perch (*Stizostedion lucioperca* L.) in the Helsinki sea area. *Finnish Fisheries Research* **3,** 1-12.

Lehtonen, H., Hansson, S., Winkler, H. (1996) Biology and exploitation of pikeperch, *Stizostedion lucioperca* (L.), in the Baltic Sea area. *Annales Zoologici Fennici* **33,** 525-535.

Lind, E.A. (1977) A review of pikeperch (*Stizostedion lucioperca*), Eurasian perch (*Perca fluviatilis*), and ruff (*Gymnocephalus cernua*) in Finland. *Journal of the Fisheries Research Board of Canada* **34,** 1684-1695.

Lobón-Cerviá, J., Montañés, C., de Sostoa, A. (1986) Reproductive ecology and growth of a population of brown trout (*Salmo trutta* L.) in an aquifer-fed stream of Old Castile (Spain). *Hydrobiologia* **135,** 81-94.

Nicola, G.G., Almodóvar, A. (2002) Reproductive traits of stream-dwelling brown trout *Salmo trutta* in contrasting neighbouring rivers of central Spain. *Freshwater Biology* **47,** 1353-1365.

Øxnevad, S.A., Heibo, E., Vøllestad, L.A. (2002) Is there a relationship between fluctuating asymmetry and reproductive investment in perch (*Perca fluviatilis*)? *Canadian Journal of Zoology* **80,** 120-125.

Parker, B.R., Schindler, D.W., Wilhelm, F.M., Donald, D.B. (2007) Bull trout population responses to reductions in angler effort and retention limits. *North American Journal of Fisheries Management* **27,** 848-859.

Paul, A.J., Post, J.R., Stelfox, J.D. (2003) Can anglers influence the abundance of native and nonnative salmonids in a stream from the Canadian Rocky Mountains? *North American Journal of Fisheries Management* **23,** 109-119.

Pierce, R.B., Tomcko, C.M. (2003) Interrelationships among production, density, growth, and mortality of northern pike in seven north-central Minnesota lakes. *Transactions of the American Fisheries Society* **132,** 143-153.

Pierce, R.B., Tomcko, C.M. (2005) Density and biomass of native northern pike populations in relation to basin-scale characteristics of north-central Minnesota lakes. *Transactions of the American Fisheries Society* **134,** 231-241.

Pierce, R.B., Tomcko, C.M., Margenau, T.L. (2003) Density dependence in growth and size structure of northern pike populations. *North American Journal of Fisheries Management* **23,** 331-339.

Pierce, R.B., Tomcko, C.M., Schupp, D.M. (1995) Exploitation of northern pike in seven small north-central Minnesota lakes. *North American Journal of Fisheries Management* **15,** 601-609.

Post, J.R., Mushens, C., Paul, A., Sullivan, M. (2003) Assessment of alternative harvest regulations for sustaining recreational fisheries: model development and application to bull trout. *North American Journal of Fisheries Management* **23,** 22-34.

Rónyai, A. (2007) Induced out-of-season and seasonal tank spawning and stripping of pike perch (*Sander lucioperca* L.). *Aquaculture Research* **38,** 1144-1151.

Schlumberger, O., Proteau, J.P. (1996) Reproduction of pike-perch (*Stizostedion lucioperca*) in captivity. *Journal of Applied Ichthyology* **12,** 149-152.

Swales, S. (1986) Population dynamics, production and angling catch of brown trout, *Salmo trutta*, in a mature upland reservoir in mid-Wales. *Environmental Biology of Fishes* **16,** 279-293.

Swales, S., Fish, J.D. (1986) Angling catch returns as indicators of the status of upland trout lakes. *Aquaculture and Fisheries Management* **17,** 75-93.

Treasurer, J. (1993) The population biology of perch, *Perca fluviatilis* L., in simple fish communities with no top piscivore. *Ecology of Freshwater Fish* **2,** 16-22.

Treasurer, J.W. (1981) Some aspects of the reproductive biology of perch *Perca fluviatilis* L. Fecundity, maturation and spawning behaviour. *Journal of Fish Biology* **18,** 729-740.

Treasurer, J.W., Owen, R., Bowers, E. (1992) The population dynamics of pike, *Esox lucius*, and perch, *Perca fluviatilis*, in a simple predator-prey system. *Environmental Biology of Fishes* **34,** 65-78.

van Poorten, B.T., Post, J.R. (2005) Seasonal fishery dynamics of a previously unexploited rainbow trout population with contrasts to established fisheries. *North American Journal of Fisheries Management* **25,** 329-345.

Wilberg, M.J., Bence, J.R., Eggold, B.T., Makauskas, D., Clapp, D.F. (2005) Yellow perch dynamics in southwestern Lake Michigan during 1986–2002. *North American Journal of Fisheries Management* **25,** 1130-1152.

Willis, D.W. (1989) Proposed standard length-weight equation for northern pike. *North American Journal of Fisheries Management* **9,** 203-208.

Ylikarjula, J., Heino, M., Dieckmann, U., Kaitala, V. (2002) Does density-dependent individual growth simplify dynamics in age-structured populations? A general model applied to perch, *Perca fluiatilis*. *Annales Zoologici Fennici* **39,** 99-107.

Paper IV

IV

Johnston, F. D., B. Beardmore, and R. Arlinghaus *Submitted*. Optimal management of diverse recreational fisheries in the presence of hooking mortality and noncompliance. Canadian Journal of Fisheries and Aquatic Sciences

Revised manuscript now published: Johnston, F. D., Beardmore, B., and Arlinghaus, R., 2015. Optimal management of recreational fisheries in the presence of hooking mortality and noncompliance — predictions from a bioeconomic model incorporating a mechanistic model of angler behavior. Canadian Journal of Fisheries and Aquatic Sciences 72(1):37–53

Optimal management of diverse recreational fisheries in the presence of hooking mortality and noncompliance

Fiona D. Johnston[1,2] , Ben Beardmore[1,3], and Robert Arlinghaus[1,2]

[1] Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany

[2] Chair for Integrative Fisheries Management, Department for Crop and Animal Sciences, Faculty of Agriculture and Horticulture, Humboldt-Universität zu Berlin, Philippstrasse 13, Haus 7, 10115 Berlin, Germany

[3] Center for Limnology, University of Wisconsin-Madison, Madison, WI 53706-1492, USA.

ABSTRACT

To systematically investigate how hooking mortality and regulatory noncompliance influence management outcomes across a range of freshwater fish species exploited by diverse angler types, we developed a bioeconomic model that integrated realistic angler behaviour with an age-structured fish population. Increased hooking mortality generally decreased socially optimal input and output regulations, (license numbers and minimum-size limits, respectively). However, the biological impacts of elevated hooking mortality strongly varied with fish species and angler type. Noncompliance was of limited importance when regulations were socially optimal, except for fish species with low compensatory reserves. However, under unlimited effort, noncompliance facilitated recruitment overfishing and increased the minimum-size limit required to avoid it. Despite added mortality from hooking and noncompliance, socially optimal management usually safeguarded biological sustainability because angler utility was strongly dependent on catch rates, but social welfare was eroded. Ignoring hooking mortality and noncompliance when predicting optimal regulations often led to population collapse. Thus, models designed to derive recommendations for recreational fisheries management must consider both hooking mortality and noncompliance. Otherwise, dissatisfied anglers or biologically overfished stocks are expected.

Keywords: bioeconomic model; compliance; discard mortality; discrete choice model; life history; depensation; angler-effort dynamics; utility

INTRODUCTION

Size-based harvest regulations and bag limits are tools commonly used in recreational fisheries to maintain fish populations at biologically sustainable levels and to meet social objectives (Radomski et al. 2001). Most output control measures are only effective if released fish survive and successfully reproduce (Arlinghaus et al. 2007, Coggins et al. 2007). Hooking mortality associated with catch-and-release (C&R) can be close to zero if injury is minimized and environmental variables are favourable (Arlinghaus et al. 2007, Hühn and Arlinghaus 2011, Muoneke and Childress 1994). However, when conditions are less favourable, such as when fish are brought to the surface from great depth, hooking mortality estimates as high as 90% have been reported for some species (Bartholomew and Bohnsack 2005, Hühn and Arlinghaus 2011). Furthermore, in some species there are non-lethal consequences of C&R for fish behaviour, growth, and reproduction (e.g., Arlinghaus et al. 2007, Richard et al. 2013). Effective management using harvest regulations therefore demands that the downsides of C&R are taken into consideration (Coggins et al. 2007, Post et al. 2003, Woodward and Griffin 2003).

An additional source of mortality generally unaccounted for in recreational fisheries stems from noncompliance with regulations (Paragamian 1984, Post 2013, Post et al. 2002). Noncompliance may not simply be the result of deliberate illegal harvest, but may also be due to measurement error or lack of regulation awareness (Page et al. 2004, Page and Radomski 2006). Noncompliance with bag limits may be low (e.g., 7%; Wilberg 2009) because anglers rarely reach these limits (Baccante 1995, Radomski et al. 2001, Wilberg 2009). By contrast, noncompliance with length-based harvest regulations can be very high in some cases (e.g., > 50%; Glass and Maughan 1984, Pierce and Tomcko 1998, Sullivan 2002). Noncompliance can also constitute a depensatory process that increases the per capita mortality probability as catch rates, and underlying populations, decline (Näslund et al. 2010, Sullivan 2002). Thus, Post et al. (2002) and Post (2013) have warned that noncompliance may be an important component contributing to the collapse of recreational fisheries. Indeed, depending on the life-history characteristics of the species, even the most restrictive regulations (e.g., zero harvest) will be ineffective if fishing effort and hooking mortality (Coggins et al. 2007, Paul et al. 2003, Post et al. 2003) or noncompliance (Gigliotti and Taylor 1990) are sufficiently high. Thus, accounting for both sources of "cryptic mortality" (Coggins et al. 2007) is important for ensuring the sustainability of recreational fisheries, yet few fisheries models do so explicitly.

Numerous factors affect the level of hooking mortality a fish population experiences, (e.g., fishing gear used, handling, fish species) (Arlinghaus et al. 2007, Bartholomew and Bohnsack 2005), some of which will vary with the type of angler attracted to a particular fishery. For example, survivorship of fish released by more experienced anglers may be higher due to better fish handling practices (e.g., Diodati and Richards 1996, Landsman et al. 2011, Meka 2004). More specialized anglers may also be less harvest-oriented and thus more likely to practice voluntary C&R (Bryan 1977, but see Dorow et al. 2010 for exceptions, Hahn 1991), which has implications for hooking mortality rates. Noncompliance rates can also be influenced by angler experience, as novice anglers are more likely to misidentify fish or be unaware of angling regulations (Schill and Kline 1995, Schmetterling and Long 1999). Furthermore, heterogeneity in fishing preferences among angler types influences their perception of fishery quality, which affects angler effort and fishing mortality (Johnston et al. 2010, 2013). There is an increasing recognition that consideration angler behaviour is crucial for predicting management strategies for recreational fisheries (Abbott and Fenichel 2013, Fenichel et al. 2013, Johnston et al. 2010). Thus, explicitly considering the composition of

the angling population is likely also important when predicting the effects of hooking mortality and noncompliance on recreational fisheries.

Previous research on the influence of hooking mortality (Risley and Zydlewski 2010, Waters and Huntsman 1986, Woodward and Griffin 2003) and noncompliance (Gigliotti and Taylor 1990, Henderson and Fabrizio 2013, Post et al. 2003) on the efficacy of angling regulations for achieving management objectives, and on optimal management strategies (Coggins et al. 2007, Henderson 2009, Pine et al. 2008), have not considered some important factors. For example, most available studies on hooking mortality and regulatory noncompliance have not treated angler behaviour as dynamic (but see Post et al. 2003, Woodward and Griffin 2003 for exceptions), or accounted for the variable effort responses associated with diverse angler types. Moreover, many of the available studies focus on single species, with only a few (e.g., Coggins et al. 2007, Pine et al. 2008) explicitly accounting for diversity in fish life history, which is important for determining the resiliency of a species to overexploitation. Finally, past studies have defined "optimal" regulations based on yield (i.e., maximum sustainable yield, MSY), ignoring the multiple attributes that influence angler satisfaction and utility. By contrast, optimal social yield (OSY) incorporates social and economic benefits provided by a fishery to anglers that are not measured by fish yield alone (Malvestuto and Hudgins 1996, Radomski et al. 2001, Roedel 1975). By considering anglers' preferences more explicitly, more realistic management objectives, such as OSY, can be constructed and the regulations to support them can be determined (Cox et al. 2003, Johnston et al. 2010, 2013).

In this study, we investigated the importance of accounting for the hidden mortality from hooking and noncompliance using a dynamic bioeconomic model that predicts the combination of input (e.g., license number) and output (e.g., minimum-size limit, MSL) regulations that provide the greatest social welfare (i.e., OSY) to a heterogeneous angling community across a range of fish species. The model incorporated dynamic fish and angler populations using a range of fish life-history types (LHTs) and angler types to investigate the generality of our findings. A discrete choice model, based on empirical data, added realism to the behavioural model used to predict angler effort, improving our representation of fish-angler dynamics when compared to our previous work, which was based on entirely hypothetical angler types (Johnston et al. 2010, 2013). With the resulting model, we evaluated how hooking mortality and noncompliance influenced predictions about; i) the biological impacts of fishing, ii) socially optimal regulations, iii) the biological and social conditions under optimal regulations, and iv) the potential consequence for the biological sustainability of the fishery if hooking mortality and noncompliance were ignored or if the fishery was not managed in a socially optimal manner. Overall, the study's objective was to improve our understanding about the effect of hooking mortality and noncompliance on management outcomes and their importance for the determination of optimal input and output regulations across a range of recreationally important fish species.

METHODS

We investigated the importance of accounting for mortality from hooking and noncompliance using the bioeconomic modelling approach described by Johnston et al. (2010, 2013), which was adapted to include empirically described anglers. The model framework includes a deterministic age-structured biological component, which describes the dynamics of the fish population, a social component, which describes the dynamic response of the angler population to changes in fishery attributes (e.g., catch rates, size of fish caught, crowding, regulations), and a management component, which allows for the application of both input (e.g., license numbers) and output regulations (e.g., minimum-size limits, MSLs; Figure 1).

Model results predict the combination of MSL and license number that provides the greatest aggregate social welfare to the angling community using the economic utility concept. Model equations and variables can be found in the appendix (Tables A1-A4). Parameter values describing the fish LHTs modelled are provided in the Table S1 of the supplementary material.

Biological component

Details of the biological model can be found in Johnston et al. (2010, 2013), and we provide only a brief summary here. In short, the biological submodel included the most salient processes that described the life-history characteristics of the fish population under investigation. We simulated an age-structured fish population model with annually pulsed reproduction and multiple density-dependent feedbacks. We included, density-dependent survival of the early life-stage (spawning to post-hatch) through a stock-recruitment relationship, and (ii) density-dependent growth in body size, both of which are important for determining the compensatory response of fish to exploitation from angling (Lorenzen 2008, Lorenzen and Enberg 2002). To account for the size-dependent processes inherent in a fishery (Lewin et al. 2006), a sigmoidal vulnerability curve was used to determine vulnerability of fish to capture, and MSLs based on length were used to determine which fish were legally harvestable. Fish reproduction was assumed to occur on an annual basis at the beginning of each year as is typical for most fishes from temperate regions. However, fish mortality and growth in body size were described by continuous functions to account for growth into vulnerable and legally harvestable sizes within each year, and for the recapture and repeated exposure to hooking mortality of released individuals throughout the fishing season, both of which are important aspects of recreational fisheries models (Coggins et al. 2007).

To examine how impacts of hooking mortality and noncompliance might differ with fish life history, five prototypical fish life-history types (LHTs), described in detail in Johnston et al. (2013), were used in this study: brown trout (*Salmo trutta*), bull trout (*Salvelinus confluentus*), European perch (*Perca fluviatilis*), northern pike (*Esox lucius*), and pikeperch (*Sander lucioperca*). These LHTs were chosen because they represent the broad range of diverse life-history characteristics (see Table S1 and Johnston et al. 2013 for details) of species commonly targeted by freshwater recreational anglers (e.g., Almodóvar and Nicola 2004, Beardmore et al. 2011, Post et al. 2002). According to our previous research, LHTs had different intrinsic vulnerabilities to overexploitation, being least to greatest as follows; perch, brown trout, pikeperch, pike, and bull trout (Johnston et al. 2013).

Social component

The model structure of Johnston et al. (2010) was designed to allow for the integration of a discrete choice model to describe multi-dimensional catch and non-catch related preferences and resulting behaviours of the angler population. Choice experiments are a survey tool commonly used to derive respondents' relative preferences for attributes (such as catch rate) of a desired good (e.g., an angling day), and are particularly valuable for predicting behavioural responses to novel scenarios such as the introduction of new management regulations (Beardmore et al. 2013, Ben-Akiva and Lerman 1985). Thus, angler behaviour can be predicted as a function of the attributes of the angling experience. Annual angling effort in our behavioural submodel was determined by the previous year's fishing experiences (i.e., fishery quality) and occurred at the beginning of each year. To make predictions more realistic, instead of using the prototypical angler types (generic, consumptive, and trophy

anglers) from our previous studies (Johnston et al. 2010, 2013), the angler types used here were based on results from a discrete choice experiment carried out on anglers from the German state of Mecklenburg-Vorpommern, M-V (Beardmore et al. 2013). The following fishery attributes were included in the survey: expected number, average size and maximum size of fish caught, the number of other anglers seen while fishing (i.e., crowding), MSL, daily bag limit, license fees to fish within the state of M-V, one-way travel distance, main target species, and an attribute describing the biological status of the fish stock. The so-called part-worth utility of all these attributes (determined from the choice model regression coefficients) combine to determine the overall utility an angler derives from fishing.

Using a latent class modelling analysis (Swait 1994), Beardmore et al. (2013) found that the preference diversity of anglers sampled in M-V was best described when they were allocated into three classes (angler types), with class-1, class-2, and class-3 anglers comprising 58%, 33% and 9% of the sample, respectively. Assignment to a particular angler type group (class membership) was largely determined by the centrality of angling to a respondent's lifestyle and the respondent's self-reported level of commitment to fishing (Beardmore et al. 2013), which can be interpreted as a subdimension of the angler specialization continuum (Bryan 1977). The three angler types, thus, represented three classes of differentially specialized anglers that differed in their preferences for selected fishery attributes (Figure 2). Furthermore, the angler types varied in their propensity to voluntarily release fish, with class-1 anglers and class-2 anglers being similarly harvest-oriented, and class-3 anglers being much less consumptive (see Table A4 for details). Thus, class-1 anglers represented very committed and consumptive anglers (hereafter referred to as committed anglers for simplicity), class-2 anglers were casual, consumptive anglers (hereafter referred to as casual anglers), and class 3 anglers were less consumptive and more trophy-oriented (hereafter referred to as trophy anglers).

The incorporation of the three angler types described by Beardmore et al. (2013) into the modelling framework of Johnston et al. (2010, 2013) required calibration. Variation of attribute levels for catch characteristics (number, average size, and maximum size of fish caught) and crowding presented to anglers in the choice experiment by Beardmore et al. (2013) were species specific, and based on means and standard deviations estimated from diary information for these attributed collected from anglers in the study region. Regression coefficients were estimated on z-transformed attributes to remove species-specific variation in absolute values for the catch-related attributes. Hence, to calibrate the behavioural component of our model to a specific LHT, we scaled the choice model to the average values and the variation of catch-related attributes that could be expected given the parameter set used to describe each LHT. To that end, we replaced the means and standard deviations used by Beardmore et al. (2013) with ones suitable for our modelled LHTs (Table A3). This was a reasonable approach given that the coefficients of the choice model reflected utility changes in catch-related attributes relative to an average species-specific fishing experience. For each LHT, we chose mean values for average daily catch, average size, and maximum size of fish caught to be values estimated when the population was in a state that maximized harvested biomass (maximum sustainable yield, MSY). For each LHT, we then randomly drew 500 fixed effort levels from a normal distribution, which had a mean equal to the effort at MSY and a standard deviation that was based on the assumption that a low effort level of 5 h ha^{-1} constituted the lower 95% confidence interval of the distribution. Catch attributes at each level of effort were then determined (assuming no MSL or daily bag limit, harvest of all caught fish, and zero hooking mortality and noncompliance), and the variation across the 500 samples was used to determine an average coefficient of variation (CV) across LHTs. The CV and mean were used to calculate the standard deviation for each LHT, which was then

used in the implementation of the parameter set by Beardmore et al. (2013) to the model environment (Table A3). Similarly, mean daily crowding was set at the average values reported for perch, pike and pikeperch by Beardmore et al. (2013), and brown trout was assumed to be identical to perch and pikeperch, and bull trout the same as pike. The mean values and average CV for daily crowding taken from angler diary data (averaged across pike, perch and pikeperch, *Beardmore, Unpublished data*), and used to calculate species-specific standard deviations of crowding (Table A3).

In addition to the calibration process, adjustments were made to the part-worth utility (PWU) function for average daily catch rate, MSL and daily bag limits. In particular, PWU functions for MSLs and daily bag limits were designed to represent continuous functions rather than discrete ones, as in the original stated preference survey by Beardmore et al. (2013), to facilitate their interface with quantitative model outputs, which served as inputs into the angler behavioural model. In addition, because the range of attribute levels tested by Beardmore et al. (2013) did not include extremely low catch levels or very high MSLs that result in complete mandatory C&R, we extrapolated the PWU functions for average daily catch and MSL beyond the range reported by Beardmore et al. (2013) following the reasonable assumption that extremely low catch rates would not be welcomed by anglers (Cox et al. 2003) and that very restrictive harvest regulations would similarly entail aversion (Johnston et al. 2011). Detailed methods for these adjustments are included in the Appendix. The resulting PWU functions for all attributes are depicted in Figure 2.

Variation in distance, license costs, daily bag limit, stock status, and the proportion of effort directed towards preferred species were not investigated in this study. Thus, levels of these attributes were constant for all simulations (see Table A3).

Outline of analyses

Our model was representative of a single-lake fishery, such as those run by angling clubs in central Europe, in which club managers can manipulate the fish-angler interactions by input or output regulations (Daedlow et al. 2011). Within this management framework, we investigated the impact of hooking mortality and noncompliance on regulation outcomes across a range of LHTs and for diverse angler types. A recent review by Hühn and Arlinghaus (2011) on hooking mortality rates of European species important for recreational fisheries, or related species, found that the majority (57.1%) of hooking mortality estimates were under 10%, and that estimates rarely (7.9 %) exceeded 50%. Reflecting this distribution, we explored the importance of considering hooking mortality for socially optimal recreational fisheries management by considering five different levels of hooking mortality $f_{\mathrm{h}j}$ (0%, 5%, 10%, 25%, and 50%, Table A2), in the presence and absence of noncompliance mortality $f_{\mathrm{n}j}$. When present, the percent illegal harvest was calculated using an empirical relationship similar to the one described by Sullivan (2002) for walleye (*Sander vitreus*) recreational fisheries, $f_{\mathrm{n}j} = \gamma\ CPUE^{\varsigma} / 100$, where CPUE is the hourly catch rate of walleye protected by size limits, $\gamma = 1.25$, and $\varsigma = -0.84$. Sullivan (2002) found that noncompliance was inversely related to CPUE, resulting in a depensatory response to fishery decline (Post et al. 2002). To account for differences in catch rates of protected fish among LHTs compared with catch rates of protected walleye from the study by Sullivan (2002), the γ parameter was customized to each LHT so that the noncompliance function was comparable across LHTs (perch $\gamma = 3.31$, brown trout $\gamma = 1.92$, pikeperch $\gamma = 0.95$, pike $\gamma = 0.33$, bull trout $\gamma = 0.19$). To that end, the ratio between the catch rate under mandatory

C&R conditions of each LHT and the catch rate under mandatory C&R conditions of walleye (assumed to be 1.3 h^{-1} for walleye, see Figure 2 in Sullivan, 2002), was used to adjust γ so that the percentage illegal harvest at the catch rate under mandatory C&R regulations was the same for all LHTs and the walleye from Sullivan's study. The exponential term ς was held constant for all LHTs. It should be noted that the adjusted relationship calculated for pikeperch, a species closely related to walleye, was very similar to the relationship presented by Sullivan (2002) for walleye.

At a given level of hooking mortality and noncompliance (presence/absence), simulations were run across a range of MSLs and license numbers (Table A2) for homogeneous angler populations composed of one angler type (class-1, -2, or -3), and for a mixed population composed of all three angler types in proportion to the relative composition reported by Beardmore et al. (2013) (Table A4). Anglers responded dynamically to the perceived quality of the fishery through the effect of utility on the angler's probability of fishing (Table A1, equation 2a). The combination of MSL and license number that maximized the total utility, defined as the greatest social welfare to the angling community, (Table A1, equation 7b) was considered to be the socially optimal regulations for that scenario (MSL_{opt} = optimal MSL, $A_{L\ opt}$ = optimal license number). We evaluated how differing levels of hooking mortality and noncompliance influenced predictions about optimal regulations and the biological impacts of fishing across angler populations and LHTs. Biological impacts were evaluated using a weighted spawning-potential ratio (Table A1, Equation 7a), which is commonly used to assess the likelihood of recruitment overfishing (Allen et al. 2013, Allen et al. 2009, Coggins et al. 2007). SPR values below 0.2–0.3 are considered critical (Goodyear 1993), whereas maintaining SPR above 0.35–0.40 is likely to prevent recruitment overfishing (Clark 2002, Mace 1994). Changes in optimal regulations and the biological and social conditions (SPR and total utility) at optimal regulations for different levels of hooking mortality and noncompliance were examined for trends and compared across angler populations and LHTs.

In addition to examining how predictions about optimal regulations differed among hooking mortality and noncompliance levels, we also examined two scenarios when recreational fisheries were not managed optimally. In the first case, we examined what the biological and social consequences would be if mortality from hooking and noncompliance were ignored when predicting optimal regulations. In this scenario, the regulations predicted to be optimal if hooking mortality was 0% and noncompliance was absent were used, but hooking mortality and noncompliance were then allowed to occur in the model simulations. This scenario mimicked an optimistic manager's assumption that hooking mortality and noncompliance would be absent when in fact they were present. In the second case, we address the fact that directly limiting angling effort is not always possible, such as in open-access fisheries (Cox and Walters 2002a). Thus, we assumed that the recreational fishery was "open access" and set license number at the maximum possible in our model. We then evaluated the biological consequences of liberal input regulations at three different levels of hooking mortality (0, 10, and 25%) across the range of MSL levels modelled previously (Table A2) in the presence and absence of noncompliance.

Overall, our modelling exercise was meant to provide strategic rather than tactical insights into a particular fishery and was therefore not calibrated to the life history of a particular fish population. Any user of our model is advised to calibrate it to the utility function of local anglers and the life-history parameters of the targeted fish population when intending to derive concrete predications, e.g., the exact level of a socially optimal harvest regulation.

RESULTS

Influence of cryptic mortality on biological sustainability

The negative biological impacts of hooking mortality when anglers were fully compliant with regulations varied with the LHT and the angler type (Figure 3). Figure 3 shows that increased hooking mortality reduced the range of regulations that averted recruitment overfishing. However, for the intrinsically more resilient LHTs – perch and brown trout – only very high levels of hooking mortality (50%) altered the negative biological impacts of recreational angling compared to situations without cryptic mortality. By contrast, any increase in hooking mortality generally decreased the number of regulation combinations that averted recruitment overfishing of the more vulnerable LHTs – pikeperch, pike, and bull trout – relative to situations without cryptic mortality.

The composition of the angler population was also important for determining the negative biological impacts of angling on LHTs at a given level of hooking mortality (Figure 3). Of all angler populations, those composed solely of, or dominated by, committed anglers had the most severe biological impacts on the fish population over the range of regulations tested, regardless of hooking mortality level or LHT. By contrast, the angler population having the least impact differed with LHT. The range of regulations that resulted in recruitment overfishing was generally the narrowest if the trophy angler population targeted the less vulnerable LHTs (brown trout and pikeperch), whereas for the more vulnerable LHTs (pike and bull trout) this occurred when fished by a casual angler population. Note that neither casual nor trophy angler populations resulted in any critical SPR values for the highly resilient perch LHT.

The introduction of Sullivan-type noncompliance, surprisingly, had very little effect on the biological status of the exploited population, when judged in terms of the proportion of simulation runs that resulted in recruitment overfishing (Figure 3). Only for the more vulnerable LHTs (pike and bull trout), did the presence of noncompliance slightly reduced the number of regulation combinations that resulted in a biologically sustainable population.

Influence of cryptic mortality on socially optimal regulations

MSL_{opt}, in the absence of noncompliance, was generally either consistently low or declined as hooking mortality increased. However, the pattern strongly depended on the composition of the angler population and the LHT exploited (Figure 4). The MSL_{opt} of angler populations composed solely, or dominated by, committed anglers, experienced small to moderate (< 15% of L_{max}) declines in MSL from similar base levels as hooking mortality increased, and results were similar across LHTs. By contrast, when the trophy angler population targeted the inherently more vulnerable LHTs (bull trout, pike and pikeperch), MSL_{opt} was relatively high (> 70% of L_{max}) in the absence of cryptic mortality and then declined dramatically (~50% of L_{max}) as hooking mortality increased in the absence of noncompliance. Yet, when trophy anglers targeted the more resilient LHTs (perch and brown trout), MSL_{opt} was generally low/liberal (< 30% of L_{max}) for all levels of hooking mortality. For the casual angler population, base level MSL_{opt} in the absence of cryptic mortality was strongly species specific and less clearly linked to the intrinsic vulnerability of a LHT. As a consequence, the effect that increased hooking mortality had on MSL_{opt} was also strongly species specific.

The influence of hooking mortality on $A_{L\ opt}$, in the absence of noncompliance, was more substantial and consistent than was observed for MSL_{opt}. Across angler populations, $A_{L\ opt}$ generally decreased with increased hooking mortality, with the magnitude being negatively

correlated with the intrinsic vulnerability of the LHT (Figure 4). For example, perch generally had the highest $A_{L\ opt}$, requiring levels of hooking mortality in excess of 10% before $A_{L\ opt}$ was affected. By contrast, bull trout generally had the lowest $A_{L\ opt}$ and even low levels of hooking mortality caused substantial reductions in $A_{L\ opt}$. Despite these general trends, the results for casual angler populations were qualitatively different than for the other angler types, with optimal license numbers being low even when hooking mortality was absent (with the exception of perch). Consequently, with the exception of perch, no large changes in $A_{L\ opt}$ for casual anglers occurred when hooking mortality increased.

Noncompliance rates under socially optimal regulations were generally low (<5%) for the intrinsically less vulnerable LHTs and higher (generally >5% and often exceeding 10%) for the more vulnerable LHTs. The inclusion of noncompliance mortality, however, did not have a large influence on predicted MSL_{opt}, with only slight differences being observed for pike and bull trout (Figure 4). However, when hooking mortality levels were low, the presence of noncompliance was important when predicting $A_{L\ opt}$ for the intrinsically more vulnerable LHTs. Accordingly, for bull trout, pike, and to a lesser extent pikeperch, $A_{L\ opt}$ at hooking mortality levels under 25% were much lower when noncompliance was present than when it was absent (Figure 4). This pattern was consistent across angler populations, although the magnitude of the effect was minimal for the casual angler population because $A_{L\ opt}$ was low even in the absence of cryptic mortality.

Biological and social conditions under socially optimal regulations

The SPR predicted under optimal regulations declined with increased hooking mortality levels, across all LHTs and angler populations, although increases in hooking mortality from 25% to 50% often did not further decrease SPR much (Figure 5). Despite these declines, with a few exceptions, SPR was maintained above 0.35 under socially optimal input and output regulations. However, in the case of bull trout fished by committed or mixed angler populations, hooking mortality $\geq$ 25% resulted in SPR levels under optimal regulations falling below 0.35, but SPR never fell below 0.20. The addition of noncompliance only resulted in slight differences being in the SPR under optimal conditions when noncompliance was present and when it was absent for pikeperch, perch and bull trout (Figure 5). In the exceptional case of bull trout fished by angler populations dominated by committed anglers, SPR levels dropped below 0.35 when hooking mortality was as low as 10% if noncompliance was present (Figure 5).

The total utility derived by the angler population was systematically eroded by hooking mortality, however, the magnitude of the effect varied with fish LHT and angler population (Figure 6). Excluding perch, declines in total utility were generally minor when LHTs were fished by a casual angler population. By contrast, when fished by the other angler populations, perch often experienced the greatest reductions and bull trout the least reductions in total utility when higher levels of hooking mortality were imposed but this trend was much less consistent under lower levels of hooking mortality. Similar to the trend seen for $A_{L\ opt}$ of the more vulnerable LHTs, the total utilities gained from fishing at hooking mortality levels under 25% were slightly lower in the presence of noncompliance than in its absence (Figure 6).

The consequences of ignoring cryptic mortality

The biological consequences, in terms of recruitment overfishing, of ignoring cryptic mortality were severe. When regulations were set at values predicted to be optimal in the absence of hooking mortality and noncompliance, but cryptic mortality was in fact present,

all LHTs except the intrinsically least vulnerable perch, experienced recruitment overfishing with SPR levels dropping well below 0.35 at some level of hooking mortality (Figure 5). As intrinsic LHT vulnerability increased, the hooking mortality level required to depress SPR to levels below 0.35 decreased (e.g., 25%-50% for brown trout and 5% for bull trout, when fished by committed anglers). Angler type also played an important role. For example, casual anglers never caused recruitment overfishing, and while all other angler types caused recruitment overfishing to some degree, the level of hooking mortality required for this to occur was much higher for trophy angler populations than angler populations dominated by committed anglers. The patterns observed in the absence of noncompliance were reinforced by the presence of noncompliance mortality, which primarily influenced the results for the most vulnerable LHTs. For example, in the case of bull trout, even when hooking mortality was assumed to be 0%, noncompliance resulted in recruitment overfishing when exploited by committed or mixed angler populations.

Importance of cryptic mortality in open-access fisheries

When we modelled the fishery as one where input regulations could not be limited, in a sense representing an open-access fishery, we found that at low MSLs the SPR fell below 0.35 for most LHTs except perch, regardless of whether hooking mortality or noncompliance were present or not (Figure 7). At moderate to high levels of MSL moving towards a total C&R fishery, recruitment overfishing could be avoided across all angler types. However, the MSL level required for this to occur systematically increased as hooking mortality increased. Furthermore, for the intrinsically more vulnerable LHTs (pikeperch, pike, and particularly bull trout), minimum sustainable MSL levels increased in the presence of noncompliance, although disparity between the MSL level predicted in the absence of noncompliance and when it was present decreased substantially as hooking mortality increased. The MSL level required to avert recruitment overfishing in the presence of hooking mortality and noncompliance was also dependent on the type of angler population fishing, generally being greatest for angler populations dominated by committed anglers and least for the casual angler population, particularly for the inherently more vulnerable LHTs.

DISCUSSION

We used a novel bioeconomic modelling approach that integrated realistic angler behaviour and single-species fish population dynamics across a range of prototypical fish species to determine how hooking mortality and noncompliance systematically influenced predictions about the socially optimal and biologically sustainable management of recreational fisheries. In contrast to earlier modelling studies that maximized yield or some catch metric (e.g., Coggins et al. 2007), we used an economically founded optimal social yield (OSY) approach in which numerous catch- and non-catch-related fishery attributes contributed jointly to the social welfare (total utility) the fishery provided to the angler population. Conceptually, OSY seems to be a better approach for the management of recreational fisheries compared to MSY (Malvestuto and Hudgins 1996, Radomski et al. 2001, Roedel 1975), because it represents the multi-dimensional aspects that determine angler well-being (Cox et al. 2003). Therefore, it is encouraging that socially optimal input and output regulations were nearly always predicted to result in biologically sustainable outcomes. For a range of fish species, we found that the two sources of cryptic and often unaccounted for mortality strongly influenced the biological impact of recreational fishing on fish populations and optimal management practices. Hence, mismanagement is likely if hooking mortality and noncompliance are not appropriately accounted for.

Our study is one of the few that considers the importance of life-history diversity when predicting the influence the hooking mortality on recreational fisheries management, and to our knowledge the only one that explicitly considers angler diversity in an integrated social-ecological modelling framework. Furthermore, our study is among the first to examine how depensatory noncompliance can influence predictions about sustainable recreational fisheries. In contrast to earlier suggestions (Post 2013, Post et al. 2002), we found regulatory noncompliance to be of relatively little concern for biological sustainability as long as one can ensure that regulations are set in a socially optimal manner, except in particular circumstances, such as when intrinsically vulnerable species are exploited by committed angler types and hooking mortality levels are low. However, when fish stocks are heavily exploited by excessive effort, such as can occur in open-access fisheries, depensatory noncompliance, in the form reported by Sullivan (2002) for walleye, can drive stocks towards recruitment overfishing, as predicted by Post et al. (2002) and Post (2013), particularly when hooking mortality is limited or absent. Thus, noncompliance may become a major issue if managers are unable to use optimal input and output controls, particularly when managing intrinsically vulnerable fish populations. Given that input controls are rarely used in recreational fisheries because they are often met with considerable opposition from anglers (Cox and Walters 2002a), regulatory noncompliance is likely a serious concern in most recreational fisheries.

Influence of hooking mortality on regulation efficacy

One important concern in recreational fisheries management is determining the conditions that result in the collapse of exploited fish stocks (Post 2013), in particular recruitment overfishing (Allen et al. 2013, Hunt et al. 2011). Numerous studies have found that cryptic sources of mortality, such as hooking mortality, can undermine the efficacy of angling regulations (e.g., Coggins et al. 2007, Pine et al. 2008, Woodward and Griffin 2003) and have other unwanted effects (e.g., Risley and Zydlewski 2010), and our study was no exception. We found that the number of combinations of input and output regulations that were predicted to avert recruitment overfishing generally declined with increased hooking mortality, but that the general pattern differed quantitatively depending angler population utilizing a particularly fishery and the LHT being exploited.

Results from our study and others (Coggins et al. 2007, Paul et al. 2003, Pine et al. 2008) suggest that fish life history plays a key role in determining the impacts that hooking mortality will have on fish populations. Consistent with results from Coggins et al. (2007), we found that hooking mortality led to a decrease in the number of regulation combinations that averted recruitment overfishing for those LHTs intrinsically more vulnerable to overexploitation (e.g., bull trout). Thus, at levels reported in the literature (mean estimates of 27.5, 7.1, 21.2, and 15.9 for pikeperch, pike, lake trout *Salvelinus namaycush* a close relative of bull trout, and salmonids in general, respectively, Hühn and Arlinghaus, 2011), hooking mortality is likely to undermine the efficacy of regulations and lead to recruitment overfishing in many cases. By contrast, the intrinsically more resilient LHTs (e.g., perch and brown trout) were only impacted when hooking mortality was 50%, which is well above reported hooking mortality estimates (mean estimates of 11.0% and 7.4% for *Perca flavescens* a close relative of yellow perch and brown trout, respectively, Hühn and Arlinghaus, 2011). These results have implications for the management of species classified as threatened or vulnerable, such as bull trout in North America (Gimenez Dixon 1996, USFWS 2013), because even low levels of hooking mortality limit the regulations that are effective at maintaining fish populations at sustainable levels (this study; Post et al. 2003). Thus, our results suggest that efforts should be directed towards gaining accurate estimates of

hooking mortality for species whose life-history characteristics make them particularly vulnerable to overfishing.

We also found that the composition of the angler population was critical for determining the quantitative influence of hooking mortality on regulation efficacy, despite the qualitative patterns being similar across LHTs. Even when propensities to release fish are similar as assumed in our model for committed and casual anglers (both preferred to harvest 4 fish daily), differences in angler preferences and thus the effort anglers exert, alter the impact different angler types have on fish populations. For example, in our study angler populations dominated by committed anglers were the only ones to impact the resilient perch LHT, albeit only at hooking mortality of 50%, because of their inherent propensity to fish more than other angler types. We also found that trophy anglers, despite being more likely to voluntarily practice C&R, generally caused recruitment overfishing over a wider range of regulations than casual anglers when targeting intrinsically vulnerable LHTs, because of the general lack of interest of casual anglers in these species. Similar findings were reported by Johnston et al. (2013) where hypothetical anglers were organized along a specialization continuum. Our results reinforce the repeated call that to manage recreational fisheries sustainably, one needs to understand more about the anglers that are utilizing the resource and their behaviour (Fenichel et al. 2013, Post 2013, Radomski et al. 2001). Without such information, assessments of the impacts of hooking mortality on the biological sustainability of fisheries can be erroneous. Moreover, as our study and others have shown different angler types react differently to changes in the fishery and may continue fishing even when fish stocks decline because of the multidimensional nature of the underlying utility function (Allen et al. 2013, Hunt et al. 2011, Post et al. 2002).

Influence of hooking mortality on optimal regulations, and social and biological outcomes

Previous investigations into the effects of hooking mortality on regulations that maximized harvested biomass (an objective inherited from commercial fisheries, Goodyear 2007) found that to maintain high fishery yield in the presence of increased hooking mortality required decreases in MSLs and fishing mortality rates (Coggins et al. 2007, Henderson 2009, Pine et al. 2008). Our results were broadly similar. Increased hooking mortality caused a general decline in MSL_{opt} and a systematic decrease in $A_{L\ opt}$, particularly for intrinsically more vulnerable LHTs. This pattern emerges because restrictive MSLs are ineffective at avoiding overharvest when hooking morality is high. Instead the number of licensed anglers and correspondingly fishing effort must be reduced, to minimize overall fishing mortality of stocks suffering from high hooking mortality. As a result, MSLs can also be reduced to levels more preferred by anglers which allow for the harvest of fish that would otherwise have been lost to hooking mortality under more stringent regulations. However, only our study demonstrates that differences in angler preferences and resulting behaviour, such as the pattern exemplified by casual anglers versus other angler types, can strongly affect the influence of hooking mortality on optimal regulations. Furthermore, the general decline in MSL_{opt} with increased hooking mortality was not consistent across LHTs and angler populations. For example, while liberal MSLs generally maximized trophy angler utility when targeting more resilient LHTs, restrictive regulations maximized their satisfaction when targeting intrinsically more vulnerable LHTs – pike and bull trout – until hooking mortality levels were sufficiently high to negate any benefits and make them ineffective. This is related, in part, to MSL being an attribute directly influencing angler utility and hence behaviour, whose effect differed among angler type. Moreover, the interplay between angling effort and specific LHT characteristics resulted in non-linear feedbacks and hence complex outcomes in terms of MSL_{opt} in relation to hooking mortality. Thus, a full understanding of

the influence of hooking mortality on the optimal management of recreational fisheries using an OSY approach necessitates LHT-specific analyses that explicitly consider of the composition of the angler population.

Despite differences in the regulations that were predicted to be socially optimal among LHTs and angler populations, these regulations were not predicted to result in recruitment overfishing, with the exception of the bull trout LHT. This is because socially optimal regulations indirectly account for the underlying status of the fish population through the strong effect that large declines in the fish population have on the catch-based attributes that contribute to angler utility. Although a clear exception, it is noteworthy that recruitment overfishing of bull trout only occurred when hooking mortality was high (≥ 25%), which is on the higher end of average hooking mortality estimates for salmonids (Hühn and Arlinghaus 2011), and when targeted by an angler population dominated by committed anglers, a dedicated angler type with a generally consumptive nature and a strong propensity to fish regardless of the fishery quality (represented by a large intercept in the utility function). Our results are good news for the fishery manager, because consistent with earlier hypothetical modelling studies (Johnston et al. 2010, 2013), the management for angler objectives such as maximizing the total utility derived by the angler population will generally produce biologically sustainable outcomes even in the presence of hidden sources of mortality.

The need for a biologically sustainable fish population to maximize angler welfare explains to some degree the variation in optimal regulations among LHTs and angler populations. The more vulnerable LHTs were not able to maintain a biologically sustainable fishery if fishing effort was high, unless MSLs were very restrictive and cryptic mortality was not sufficiently high to undermine their effectiveness. Instead, to avoid recruitment overfishing while maximizing angler utility, effort must be reduced through input controls, which consequently allows for reductions in MSLs to those more preferred by anglers. However, anglers differ in their preferences (Hunt 2005), overall commitment to angling (Beardmore et al. 2013), and consumptive-orientation (Bryan 1977), all of which influence the interplay between angling effort and specific LHT characteristics (Johnston et al. 2013), and ultimately the degree to which cryptic mortality will influence the regulations that are socially optimal. For example, the general lack of commitment to angling and their correspondingly low responsiveness to changes in fishery quality, in combination with their consumptive nature, resulted in the casual anglers generally having low $A_{L\ opt}$'s for most LHTs. Consequently, casual anglers had minimal impacts on fish stocks, regardless of the level of hooking mortality. Our results support suggestions that effort regulations may be an appropriate tool for managing recreational fisheries for biological sustainability (Cox and Walters 2002a, Cox and Walters 2002b, Post et al. 2003), particularly when hooking mortality is high (Coggins et al. 2007, Pine et al. 2008).

Our study collectively showed that the often-cited aim of many managers to maximize the satisfaction of anglers while maintaining the biological sustainability of exploited populations (Cox and Walters 2002a, Peterson and Evans 2003, Radomski et al. 2001) is systematically eroded as hooking mortality increases. We found that hooking mortality, even low levels (5%), caused large reductions in the welfare the fishery provided to the various angler types, although the magnitude of these reductions depended on fish LHT and the composition of the angler population. Similar to previous studies that found a reduction in fishery yield and harvesting efficiency as hooking mortality increased (e.g., Coggins et al. 2007, Henderson 2009, Pine et al. 2008), the loss of fish to discard mortality and the reduction in license numbers required to sustain the fish population under elevated hooking mortality led to losses

in angler welfare. The fact that large declines in total utility occurred even at the low levels of hooking mortality commonly estimated from recreational fisheries (e.g., means of 18% and 15.9% across studies, Bartholomew and Bohnsack 2005, Hühn and Arlinghaus 2011, respectively) suggest that hooking mortality broadly contributes to the erosion of the quality of most recreational fisheries. Put differently, minimizing hooking mortality by appropriate gear choice and angler behaviour can pay huge welfare dividends, and is thus in the self-interest of anglers. Therefore, if maximizing angler satisfaction is a priority of recreational managers, a focus should be placed on minimizing hooking mortality through such methods as gear restrictions, and education and outreach programs designed to reduce handling stress and injury because these actions increase post-release survival in most fish species (Arlinghaus et al. 2007, EIFAC 2008, FAO 2012).

The consequences of ignoring hooking mortality when predicting socially optimal regulations

Perhaps because obtaining accurate measures of cryptic mortality is difficult, many existing fisheries models do not consistently include hidden sources of mortality such as hooking mortality. Yet, for recreational fisheries managed using an OSY approach, ignoring hooking mortality when predicting optimal regulations is of great concern if it is, in fact, present. We found that, similar to the implementation uncertainty generated by angler behaviour (Fulton et al. 2011), ignoring hooking mortality when determining regulations potentially puts all but the most resilient LHTs at risk of recruitment overfishing. If not regulated appropriately, even hooking mortality levels below reported averages of 18% and 15.9% (Bartholomew and Bohnsack 2005, Hühn and Arlinghaus 2011, respectively) were sufficient to threaten the sustainability of fisheries of the intrinsically most vulnerable LHTs, when targeted by more committed angler types. These results are consistent with those of Coggins et al. (2007) who found that hooking mortality levels >20% led to recruitment overfishing of the intrinsically least vulnerable LHT (so called short-lived high-productivity), whereas for the more vulnerable LHT (termed long-lived low-productivity), hooking mortality levels of 5% were already of source of great concern. However, the consequences of ignoring hooking mortality when predicting optimal regulations may be mediated by the angler population if it is composed of less committed angler types, such as our casual anglers, for whom optimal license numbers were generally low. These results add further weight to the general conclusion that to gain more robust predictions about the socially optimal management of recreational fisheries hooking mortality needs to be explicitly considered within the context of the targeted LHT and types of anglers fishing. Otherwise, regulations might be either too stringent or too liberal, resulting in overfished stocks or socially suboptimal outcomes (Fenichel et al. 2013; this study, Johnston et al. 2010).

The importance of hooking mortality in open-access fisheries when optimal management is not possible

Unfortunately, many recreational fisheries, particularly in North America, are open access (Cox and Walters 2002a, Post 2013) and, thus, effort cannot be regulated in an optimal manner. In such cases, managers are left to regulate fisheries solely by output controls such as MSLs or other size-based harvest limits often used to minimize fishing mortality (Johnson and Martinez 1995, Lewin et al. 2006, Radomski et al. 2001). We found that if effort was uncontrolled, liberal MSLs were rarely sufficient to avoid recruitment overfishing in all but the most resilient LHTs, similar to other studies (Allen et al. 2013), regardless of whether hooking mortality was present or not. The introduction of hooking mortality resulted in the systematic erosion the range of MSLs that averted recruitment overfishing, but the magnitude of this effect was strongly dependent on the intrinsic vulnerability of the LHT, as reported in

other studies (Coggins et al. 2007, Pine et al. 2008), and the composition of the angler population. For example, because trophy anglers were much less consumptively-oriented, hooking mortality levels as high as 25% did not result in recruitment overfishing of the brown trout-like LHT under any MSL regulation, whereas they did for all other angler populations. We found MSLs predicted to be sustainable in the absence of hooking mortality may not produce sustainable outcomes when hooking mortality is present. Where the disparity between sustainable and unsustainable occurs is often at MSL levels currently used in many recreational fisheries. MSLs are often set as low as possible to minimize the loss of potential harvest to natural mortality (Johnson and Martinez 1995), but high enough to allow most fish to spawn at least once (Diana and Smith 2008, Lewin et al. 2006). However, an MSL of 65 cm for bull trout, for example, that mature around 60 cm (Johnston and Post 2009), would, according to the parameter set used in the present paper, result in recruitment overfishing, even at low hooking mortality rates (≤ 10%), which are commonly reported for salmonids (Hühn and Arlinghaus 2011). Given the sensitivity of intrinsically more vulnerable LHTs in our model to any source of hooking mortality, more effort should be directed at obtaining accurate estimates for these species, and these estimates should be consistently integrated into models designed to predict management actions.

Influence of noncompliance on regulation efficacy, optimal regulations and social and biological outcomes

Generally we found that noncompliance either had negligible effects on model predictions, or the effect was isolated to the intrinsically most vulnerable LHTs under a narrow range of low hooking mortality levels. This is in contrast to other reports that noncompliance with angling regulations, similar to hooking mortality, undermine regulation effectiveness (Gigliotti and Taylor 1990, Henderson and Fabrizio 2013, Post et al. 2003). The reason for the different predictions between our study and other modelling studies (e.g., Gigliotti and Taylor 1990, Post et al. 2003) is that noncompliance was modelled as a depensatory process reliant on catch rates of protected fish, rather than as a constant rate. One must understand that, as we discussed in the context of open-access fisheries above, under low MSLs fishing was often unsustainable regardless of whether cryptic mortality of any kind was present or not. Thus, the addition of noncompliance when MSLs were low, despite the rates being high, did not change the status of already recruitment overfished stocks. At high MSLs, catch rates of protected fish were generally high, so correspondingly noncompliance rates were generally low. This leaves us with a very narrow intermediate MSL range where, in the absence of noncompliance the fishery was sustainable, but where in its presence catch rates were sufficiently low to cause elevated noncompliance rates. Whether this combination of events occurred was strongly dependent on the LHT being targeted and the level of hooking mortality present. In this intermediate range of MSLs, the more resilient LHTs had catch rates sufficiently high that noncompliance was low. By contrast, while the intrinsically more vulnerable LHTs experienced elevated noncompliance rates because catch rates were sufficiently low at intermediate MSLs, when hooking mortality was sufficiently high (e.g., > 10%) the population was no longer biologically sustainable even in the absence of noncompliance. Accordingly, we only saw an impact of noncompliance when hooking mortality levels were low and LHTs were intrinsically vulnerable to overfishing.

With this understanding in mind, it becomes clear why noncompliance had little influence on the social and biological outcomes under optimal regulations. When managed optimally, we found that noncompliance generally had very little influence on the biological and social conditions of the fishery, particularly for the more resilient LHTs (e.g., perch, brown trout, and to a lesser extent pikeperch). This was due to the state of the fishery under optimal

regulations; catch rates of protected fish were sufficiently high that very low noncompliance rates resulted (generally < 5% = weak depensation). By contrast, for the less resilient LHTs (e.g., pike and bull trout), catch rates of protected fish were generally lower resulting in higher noncompliance rates (often > 10% = strong depensation). To compensate for this increased source of mortality, particularly at low hooking mortality rates, optimal license levels were strongly reduced to maintain pike and bull trout populations. Thus, in general, the biological impact of noncompliance was found to be negligible compared to elevated hooking mortality for most LHTs (except bull trout) under conditions of a well-managed fishery maintained at optimal regulations. However, this does not to minimize the importance of accounting for noncompliance in fisheries management, because for intrinsically more vulnerable LHTs it can still strongly influence optimal regulations and their efficacy, particularly at the low hooking mortality levels (≤ 10%) that are commonly reported for freshwater fisheries (Hühn and Arlinghaus 2011).

In fact, if noncompliance is indeed a depensatory process (Näslund et al. 2010, Sullivan 2002), accounting for its presence can be critical for the biological sustainability of the fishery, particularly if fisheries are not managed in an optimal manner. We found that ignoring hooking mortality when setting optimal regulations, if in fact present, resulted in the recruitment overfishing of all but the most resilient LHT, perch. However, the level of hooking mortality required for overfishing to occur was reduced, substantially in the case of less resilient LTHs), when noncompliance was present. Likewise, if fishing effort was uncontrolled, accounting for noncompliance became critical, particularly in the range of MSLs currently used in many recreational fisheries and at low hooking mortality levels (0-10 %). Noncompliance accelerates the decline of already vulnerable species when fisheries are open access (Post 2013, Post et al. 2002). Our results collectively suggest that considering noncompliance is important both when setting optimal regulations and when predicting the impacts of angling on open-access recreational fisheries.

Limitations and extensions

Like any other modelling exercise, our bioeconomic model has a number of limitations that prevent the predictions being taken as face value. While we feel certain about the trends our model derives, we cannot trust single-species predictions to exactly represent outcomes to be expected on any given ecosystem. Many of the limitations of the modelling framework presented here (e.g., the single fishery rather than landscape focus of our model) were discussed by Johnston et al. (2010), 2013) and the reader is referred to these sources for a detailed account. However, one of the major limitations mentioned in these papers, the theoretical description of angler types, was addressed here by using empirical results from a stated discrete choice experiment to describe angler behaviour. However, due to limitations with the range of attribute levels tested in the choice experiment, e.g., not including sufficiently low catch rates or sufficiently high MSLs in the original angler survey, we needed to "tune" some of the coefficients and functional forms of the PWU functions from Beardmore et al. (2013) based on realistic assumptions about how anglers would behave at these extremes (e.g., at very low catch rates or at very high MSL). In the future the range of levels for attributes considered in choice experiments should be extended to allow for the integration of choice model results into a bioeconomic model framework. Along a similar vein, because only four attribute levels were tested for many attributes by Beardmore et al. (2013), the functional-form of the PWU relationships were limited to linear ones. Testing a larger number of levels would allow for the detection of more complex relationships, such as the quadratic relationships we used in our model to describe the PWU for daily catch and the angling regulations. Finally, the thresholds beyond which anglers voluntarily released fish

can strongly influence predictions depending on the LHT in question. In this study, values used were estimated from diary data from M-V anglers for perch, and it was assumed that this threshold applied across all LHTs. However, the harvesting behaviour of anglers depends on the target species (Beardmore et al. 2011, Hunt et al. 2011). For example, an angler may be more harvest-oriented when targeting perch and more trophy-oriented when targeting pike, and there might be interactions in harvesting decisions among species (Hunt et al. 2002). Such dynamics were not accounted for in the present model because we simulated a single-species fishery rather than a multi-species community. Anglers' species preferences may also be important for determining noncompliance rates, for example, with bass anglers being more compliant with regulations than non-bass anglers (Glass and Maughan 1984). Furthermore, we assumed that angler behaviour was consistent over time, which may not be the case (Baerenklau and Provencher 2005). Likewise, compliance with regulations over time may also change (but see Caroffino 2013, Näslund et al. 2010), and hooking mortality may decrease as anglers gain experience and improve their handling practices (e.g., Diodati and Richards 1996, Meka 2004). The influence of temporal changes in angler behaviour deserves further study and should be integrated in extensions of the present work.

Our representation of noncompliance was based on empirical findings by Sullivan (2002), who reported that noncompliance was lowest under mandatory catch-and-release regulations, perhaps because anglers who fished these walleye lakes had no expectation of harvest. However, recent studies suggest that noncompliance rates are positively related to the restrictiveness of regulations that require large proportions of the catch to be released, because anglers wish to harvest some fish (Caroffino 2013, Henderson and Fabrizio 2013). However, the noncompliance index used in these studies, rather than being the proportion of protected fish caught that were harvested as was used by Sullivan (2002) and in our study, was defined as the proportion of protected- versus legal-sized fish harvested, which depends on the size structure of the population in addition to illegal harvest levels (Sullivan 2002). Without a specific model that represents such noncompliance patterns, it is unclear how it would modify the results we have presented here, particularly because Sullivan (2002) found that a high proportion of illegal fish in the total harvest did not necessarily correlate with high illegal harvest rates as we defined it in our study. More research is needed to determine if noncompliance is indeed a depensatory process, simply an additive effect, or present in some other form, and once determined what the strength of the relationship is in relation to catch rate, harvest rate or regulation strictness across a range of species.

Conclusions

We found that hooking mortality strongly affected the biological and social conditions under optimal regulations, and the regulations themselves. As hooking mortality increased, the optimal angling effort declined and generally so did the optimal MSL. In particular, this is expected when the angler population is composed of more committed angler types, and may be of less concern if anglers are casual because they have little effect on stocks when their effort is not excessive or unlimited. The impact of noncompliance on the socially optimal regulations predicted was isolated to the intrinsically most vulnerable LHTs and a narrow range of hooking mortality levels, but under socially input and output regulations the impact of noncompliance on the fish stock was negligible. Despite the added mortality from C&R and noncompliance, using an OSY approach for the management of recreational fisheries, in most cases, resulted in biological sustainability. However, the changes in regulations required to maintain a sustainable fishery in the presence of cryptic mortality will lead to fisheries that are suboptimal in terms of the social welfare they produce. Furthermore, ignoring the presence of hooking mortality and noncompliance completely when setting optimal

regulations, or simply the inability to set regulations in an optimal manner such as in open-access fisheries, may result in biologically unsustainable fisheries. Under these conditions, hooking mortality increases the MSL needed to avoid recruitment overfishing, and the impact of noncompliance on recruitment overfishing becomes non-trivial, often requiring further increases in MSL to avert overexploitation. Accounting for hooking mortality and noncompliance is, thus, critical to reduce the implementation uncertainty associated with harvest regulations, and recreational-fisheries managers may need to consider input controls to a greater extent than is presently the case to maintain high quality fisheries that are also biologically sustainable.

ACKNOWLEDGEMENTS

Financial support for this study was provided by the German Ministry for Education and Research (BMBF) through the Besatzfisch-Project, a Program for Social-Ecological Research (grant no. 01UU0907, www.besatz-fisch.de), and by the Gottfried-Wilhelm-Leibniz Community through the Adaptfish Project (www.adaptfish.igb-berlin.de). We gratefully acknowledge Shuichi Matsumura for his advice during the development of this study, and Wolfgang Haider and Don Anderson for help in designing the choice experiments that were used in the present work.

LITERATURE CITED

Abbott, J.K., and Fenichel, E.P. 2013. Anticipating adaptation: a mechanistic approach for linking policy and stock status to recreational angler behavior. Can. J. Fish. Aquat. Sci. **70**(8): 1190-1208.

Allen, M.S., Ahrens, R.N.M., Hansen, M.J., and Arlinghaus, R. 2013. Dynamic angling effort influences the value of minimum-length limits to prevent recruitment overfishing. Fish. Manage. Ecol. **20**(2-3): 247-257.

Allen, M.S., Brown, P., Douglas, J., Fulton, W., and Catalano, M. 2009. An assessment of recreational fishery harvest policies for Murray cod in southeast Australia. Fish. Res. **95**(2-3): 260-267.

Almodóvar, A., and Nicola, G.G. 2004. Angling impact on conservation of Spanish stream-dwelling brown trout *Salmo trutta*. Fish. Manage. Ecol. **11**(3-4): 173-182.

Arlinghaus, R., Cooke, S.J., Lyman, J., Policansky, D., Schwab, A., Suski, C., Sutton, S.G., and Thorstad, E.B. 2007. Understanding the complexity of catch-and-release in recreational fishing: an integrative synthesis of global knowledge from historical, ethical, social and biological perspectives. Rev. Fish. Sci. **15**: 75-167.

Baccante, D. 1995. Assessing catch inequality in walleye angling fisheries. N. Am. J. Fish. Manage. **15**(3): 661-665.

Baerenklau, K.A., and Provencher, B. 2005. Static modeling of dynamic recreation behavior: Implications for prediction and welfare estimation. J. Environ. Econ. Manage. **50**(3): 617-636.

Bartholomew, A., and Bohnsack, J. 2005. A review of catch-and-release angling mortality with implications for no-take reserves. Rev. Fish Biol. Fish. **15**(1): 129-154.

Beardmore, B., Haider, W., Hunt, L.M., and Arlinghaus, R. 2011. The importance of trip context for determining primary angler motivations: are more specialized anglers more catch-oriented than previously believed? N. Am. J. Fish. Manage. **31**(5): 861-879.

Beardmore, B., Haider, W., Hunt, L.M., and Arlinghaus, R. 2013. Evaluating the ability of specialization indicators to explain fishing preferences. Leisure Sci. **35**(3): 273-292.

Ben-Akiva, M., and Lerman, S.R. 1985. Discrete choice analysis: theory and application to travel demand. . The MIT Press, Cambridge, Massachusetts.

Bryan, H. 1977. Leisure value systems and recreational specialization: the case of trout fishermen. J. Leisure Res. **9**(3): 174-187.

Caroffino, D.C. 2013. Angler compliance with lake trout length limit regulations in Great Lakes waters. N. Am. J. Fish. Manage. **33**(6): 1203-1209.

Clark, W.G. 2002. F35% revisited ten years later. N. Am. J. Fish. Manage. **22**(1): 251-257.

Coggins, L.G., Jr., Catalano, M.J., Allen, M.S., Pine, W.E., III, and Walters, C.J. 2007. Effects of cryptic mortality and the hidden costs of using length limits in fishery management. Fish Fish. **8**(3): 196-210.

Cox, S., and Walters, C. 2002a. Maintaining quality in recreational fisheries: how success breeds failure in management of open-access sport fisheries. *In* Recreational Fisheries: Ecological, Economic and Social Evaluation. *Edited by* T.J. Pitcher and C.E. Hollingworth. Blackwell Publishing, Oxford, U.K. pp. 107-119.

Cox, S.P., and Walters, C. 2002b. Modeling exploitation in recreational fisheries and implications for effort management on British Columbia rainbow trout lakes. N. Am. J. Fish. Manage. **22**(1): 21-34.

Cox, S.P., Walters, C.J., and Post, J.R. 2003. A model-based evaluation of active management of recreational fishing effort. N. Am. J. Fish. Manage. **23**: 1294-1302.

Daedlow, K., Beard Jr, T.D., and Arlinghaus, R. 2011. A property rights-based view on management of inland recreational fisheries: contrasting common and public fishing rights regimes in Germany and the U.S.A. *In* Proceedings of the 5th World Recreational Fishing Conference, American Fisheries Society Symposium 75. *Edited by* T.D. Beard Jr, R. Arlinghaus and S. Sutton. American Fisheries Society, Bethesda. pp. 13-38.

Diana, J., and Smith, K. 2008. Combining ecology, human demands, and philosophy into the management of northern pike in Michigan. Hydrobiologia **601**(1): 125-135.

Diodati, P.J., and Richards, R.A. 1996. Mortality of striped bass hooked and released in salt water. Trans. Am. Fish. Soc. **125**(2): 300-307.

Dorow, M., Beardmore, B., Haider, W., and Arlinghaus, R. 2010. Winners and losers of conservation policies for European eel, *Anguilla anguilla*: an economic welfare analysis for differently specialised eel anglers. Fish. Manage. Ecol. **17**(2): 106-125.

EIFAC. 2008. (European Inland Fisheries Advisory Commission, FAO). EIFAC Code of Practice for Recreational Fisheries. EIFAC Occasional Paper. No. 42. FAO, Rome. 45 pp.

FAO. 2012. (Food and Agricultural Organization of the United Nations). FAO Technical Guidelines for Responsible Fisheries: Recreational Fisheries. No. 13. FAO, Rome. 176 pp.

Fenichel, E.P., Abbott, J.K., and Huang, B. 2013. Modelling angler behaviour as a part of the management system: synthesizing a multi-disciplinary literature. Fish Fish. **14**(2): 137-157.

Fulton, E.A., Smith, A.D.M., Smith, D.C., and van Putten, I.E. 2011. Human behaviour: the key source of uncertainty in fisheries management. Fish Fish. **12**(1): 2-17.

Gigliotti, L.M., and Taylor, W.W. 1990. The effect of illegal harvest on recreational fisheries. N. Am. J. Fish. Manage. **10**(1): 106-110.

Gimenez Dixon, M. 1996. *Salvelinus confluentus*. *In* IUCN 2011. IUCN Red List of Threatened Species. Version 2011.2. Available from www.iucnredlist.org.

Glass, R.D., and Maughan, O.E. 1984. Angler compliance with length limits on largemouth bass in an Oklahoma reservoir. N. Am. J. Fish. Manage. **4**(4A): 457-459.

Goodyear, C.P. 1993. Spawning stock biomass per recruit in fisheries management: foundation and current use. *In* Risk Evaluation and Biological Reference Points for Fisheries Management. *Edited by* S.J. Smith, J.J. Hunt and D. Rivard. Canadian Special Publication of Fisheries and Aquatic Sciences. 120. pp. 67-81.

Goodyear, C.P. 2007. Recreational catch and release: Resource allocation between commercial and recreational fishermen. N. Am. J. Fish. Manage. **27**(4): 1189-1194.

Hahn, J. 1991. Angler specialization: measurement of a key sociological concept and implications for fisheries management decisions. Am. Fish. Soc. Symp. **12**: 380-389.

Henderson, I.M. 2009. Optimising recreational harvests of blue cod: The effects of catch-and-release mortality and size selectivity. Fish. Res. **99**(3): 184-195.

Henderson, M.J., and Fabrizio, M.C. 2013. Detecting noncompliance in the summer flounder recreational fishery using a mark–recapture growth model. N. Am. J. Fish. Manage. **33**(5): 1039-1048.

Hühn, D., and Arlinghaus, R. 2011. Determinants of hooking mortality in freshwater recreational fisheries: a quantitative meta-analysis. Am. Fish. Soc. Symp. **75**: 141-170.

Hunt, L. 2005. Recreational fishing site choice models: insights and future opportunities. Hum. Dim. Wildl. **10**(3): 153-172.

Hunt, L., Haider, W., and Armstrong, K. 2002. Understanding the fish harvesting decisions by anglers. Hum. Dim. Wildl. **7**(2): 75-89.

Hunt, L.M., Arlinghaus, R., Lester, N., and Kushneriuk, R. 2011. The effects of regional angling effort, angler behavior, and harvesting efficiency on landscape patterns of overfishing. Ecol. Appl. **21**(7): 2555-2575.

Johnson, B.M., and Martinez, P.J. 1995. Selecting harvest regulations for recreational fisheries: opportunities for research/management cooperation. Fisheries **20**(10): 22-29.

Johnston, F.D., Arlinghaus, R., and Dieckmann, U. 2010. Diversity and complexity of angler behaviour drive socially optimal input and output regulations in a bioeconomic recreational-fisheries model. Can. J. Fish. Aquat. Sci. **67**(9): 1507-1531.

Johnston, F.D., Arlinghaus, R., and Dieckmann, U. 2013. Fish life history, angler behaviour and optimal management of recreational fisheries. Fish Fish. **14**(4): 554-579.

Johnston, F.D., Arlinghaus, R., Stelfox, J., and Post, J.R. 2011. Decline in angler use despite increased catch rates: anglers' response to the implementation of a total catch-and-release regulation. Fish. Res. **110**(1): 189-197.

Johnston, F.D., and Post, J.R. 2009. Density-dependent life-history compensation of an iteroparous salmonid. Ecol. Appl. **19**(2): 449-467.

Landsman, S.J., Wachelka, H.J., Suski, C.D., and Cooke, S.J. 2011. Evaluation of the physiology, behaviour, and survival of adult muskellunge (*Esox masquinongy*) captured and released by specialized anglers. Fish. Res. **110**(2): 377-386.

Lewin, W.C., Arlinghaus, R., and Mehner, T. 2006. Documented and potential biological impacts of recreational fishing: insights for management and conservation. Rev. Fish. Sci. **14**: 305-367.

Lorenzen, K. 2008. Fish population regulation beyond stock and recruitment: the role of density-dependent growth in the recruited stock. Bull. Mar. Sci. **83**(1): 181-196.

Lorenzen, K., and Enberg, K. 2002. Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. Proceedings of the Royal Society of London, Series B **269**: 49-54.

Mace, P.M. 1994. Relationships between common biological reference points used as thresholds and targets of fisheries management strategies. Can. J. Fish. Aquat. Sci. **51**(1): 110-122.

Malvestuto, S.P., and Hudgins, M.D. 1996. Optimum yield for recreational fisheries management. Fisheries **21**(6): 6-17.

Meka, J.M. 2004. The Influence of Hook Type, Angler Experience, and Fish Size on Injury Rates and the Duration of Capture in an Alaskan Catch-and-Release Rainbow Trout Fishery. N. Am. J. Fish. Manage. **24**(4): 1309-1321.

Muoneke, M.I., and Childress, W.M. 1994. Hooking mortality: a review for recreational fisheries. Rev. Fish. Sci. **2**(2): 123-156.

Näslund, I., Eriksson, T., Hannersjö, D., Bergwall, L., Jacobsson, G., and Leonardsson, K. 2010. Time trends in angler compliance with harvest regulations in stream fisheries. Fish. Manage. Ecol. **17**(1): 52-62.

Page, K.S., Grant, G.C., Radomski, P., Jones, T.S., and Bruesewitz, R.E. 2004. Fish total length measurement error for recreational anglers: Causes and contribution to noncompliance fo the Mille Lacs walleye fishery. N. Am. J. Fish. Manage. **24**(3): 939-951.

Page, K.S., and Radomski, P. 2006. Compliance with Sport Fishery Regulations in Minnesota as Related to Regulation Awareness. Fisheries **31**(4): 166-178.

Paragamian, V.L. 1984. Angler compliance with a 12.0-inch minimum length limit for smallmouth bass in Iowa streams. N. Am. J. Fish. Manage. **4**(2): 228-229.

Paul, A.J., Post, J.R., and Stelfox, J.D. 2003. Can anglers influence the abundance of native and nonnative salmonids in a stream from the Canadian Rocky Mountains? N. Am. J. Fish. Manage. **23**(1): 109-119.

Peterson, J.T., and Evans, J.W. 2003. Quantitative decision analysis for sport fisheries management. Fisheries **28**(1): 10-21.

Pierce, R.B., and Tomcko, C.M. 1998. Angler noncompliance with slot length limits for northern pike in five small Minnesota lakes. N. Am. J. Fish. Manage. **18**(3): 720-724.

Pine, W.E., III, Martell, S.J.D., Jensen, O.P., Walters, C.J., and Kitchell, J.F. 2008. Catch-and-release and size limit regulations for blue, white, and striped marlin: the role of postrelease survival in effective policy design. Can. J. Fish. Aquat. Sci. **2008**(65): 5.

Post, J.R. 2013. Resilient recreational fisheries or prone to collapse? A decade of research on the science and management of recreational fisheries. Fish. Manage. Ecol. **20**(2-3): 99-110.

Post, J.R., Mushens, C., Paul, A., and Sullivan, M. 2003. Assessment of alternative harvest regulations for sustaining recreational fisheries: model development and application to bull trout. N. Am. J. Fish. Manage. **23**(1): 22-34.

Post, J.R., Sullivan, M., Cox, S., Lester, N.P., Walters, C.J., Parkinson, E.A., Paul, A.J., Jackson, L., and Shuter, B.J. 2002. Canada's recreational fisheries: the invisible collapse? Fisheries **27**(1): 6-17.

Radomski, P.J., Grant, G.C., Jacobson, P.C., and Cook, M.F. 2001. Visions for recreational fishing regulations. Fisheries **26**(5): 7-18.

Richard, A., Dionne, M., Wang, J., and Bernatchez, L. 2013. Does catch and release affect the mating system and individual reproductive success of wild Atlantic salmon (*Salmo salar* L.)? Mol. Ecol. **22**(1): 187-200.

Risley, C.A.L., and Zydlewski, J. 2010. Assessing the effects of catch-and-release regulations on a brook trout population using an age-structured model. N. Am. J. Fish. Manage. **30**(6): 1434-1444.

Roedel, P.M. 1975. A summary and critique of the symposium on optimal sustainable yield. *In* Optimum Sustainable Yield as a Concept in Fisheries Management. American Fisheries Society, Bethesda, MD. pp. 79-89.

Schill, D.I., and Kline, P.A. 1995. Use of Random Response to Estimate Angler Noncompliance with Fishing Regulations. N. Am. J. Fish. Manage. **15**(4): 721-731.

Schmetterling, D.A., and Long, M.H. 1999. Montana Anglers' Inability to Identify Bull Trout and Other Salmonids. Fisheries **24**(7): 24-27.

Sullivan, M.G. 2002. Illegal angling harvest of walleyes protected by length limits in Alberta. N. Am. J. Fish. Manage. **22**(3): 1053-1063.

Swait, J. 1994. A structural equation model of latent segmentation and product choice for cross-sectional revealed preference choice data. Journal of Retailing and Consumer Services **1**(2): 77-89.

USFWS. 2013. Species Information: Threatened and Endangered Animals and Plants. Available from http://ecos.fws.gov/speciesProfile/profile/speciesProfile.action?spcode=E065 [accessed 5 May 2013].

Waters, J.R., and Huntsman, G.R. 1986. Incorporating mortality from catch and release into yield-per-recruit analyses of minimum-size limits. N. Am. J. Fish. Manage. **6**(4): 463-471.

Wilberg, M.J. 2009. Estimation of recreational bag limit noncompliance using contact creel survey data. Fish. Res. **99**(3): 239-243.

Woodward, R.T., and Griffin, W.L. 2003. Size and bag limits in recreational fisheries: theoretical and empirical analysis. Mar. Resour. Econ. **18**: 239-262.

FIGURES

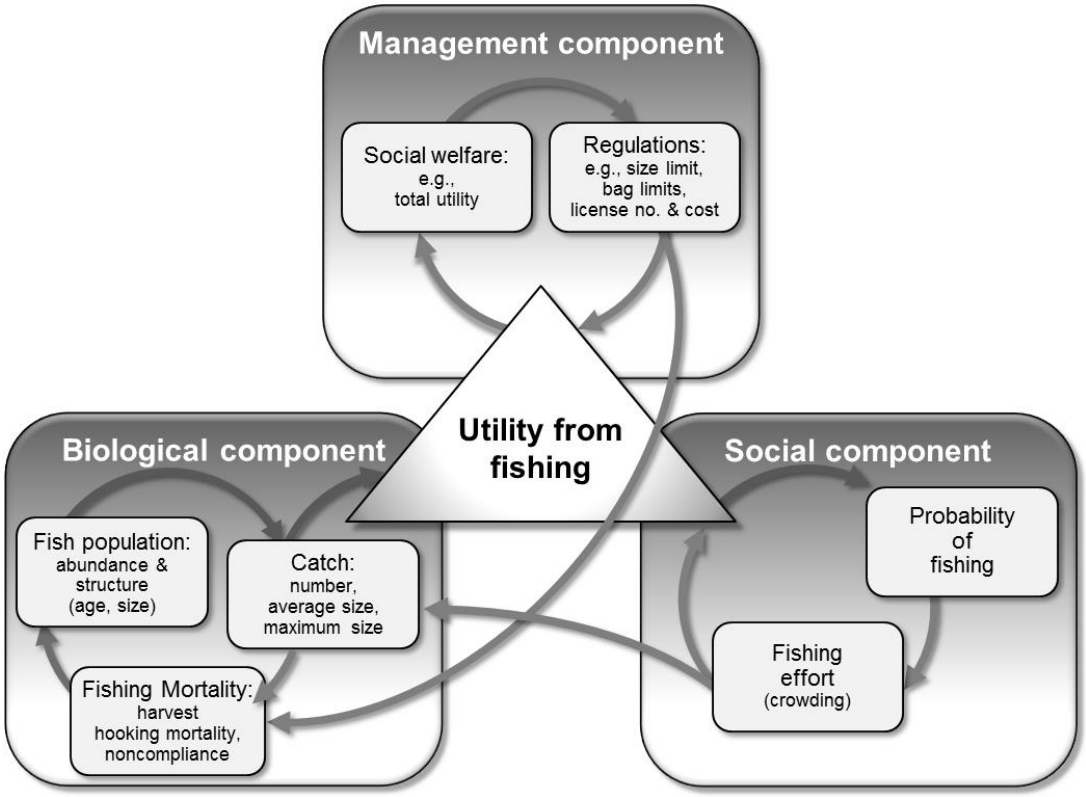


Figure 1. Schematic of modelled fishery components and their interactions.

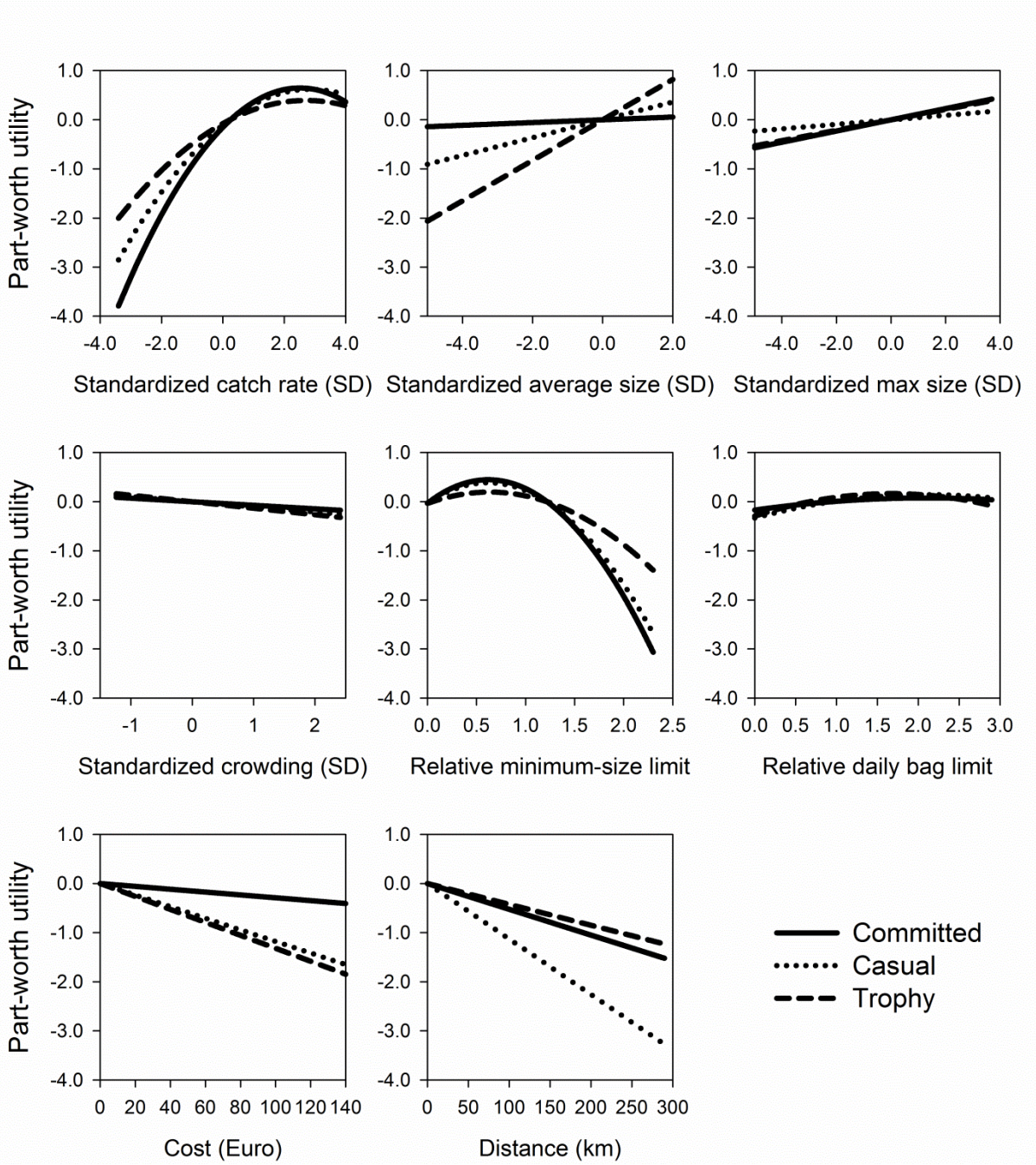


Figure 2. Part-worth-utility (PWU) functions describing the relative preferences of the three angler types described by Beardmore et al. (2013) for various fishery attributes. PWU, an economic term, is the contribution of a single fishery attribute to the total utility an angler derives from fishing, and is determined using the coefficients of the regression model from the choice experiment. See Table A3 for parameters describing these relationships. SD = standard deviation units.

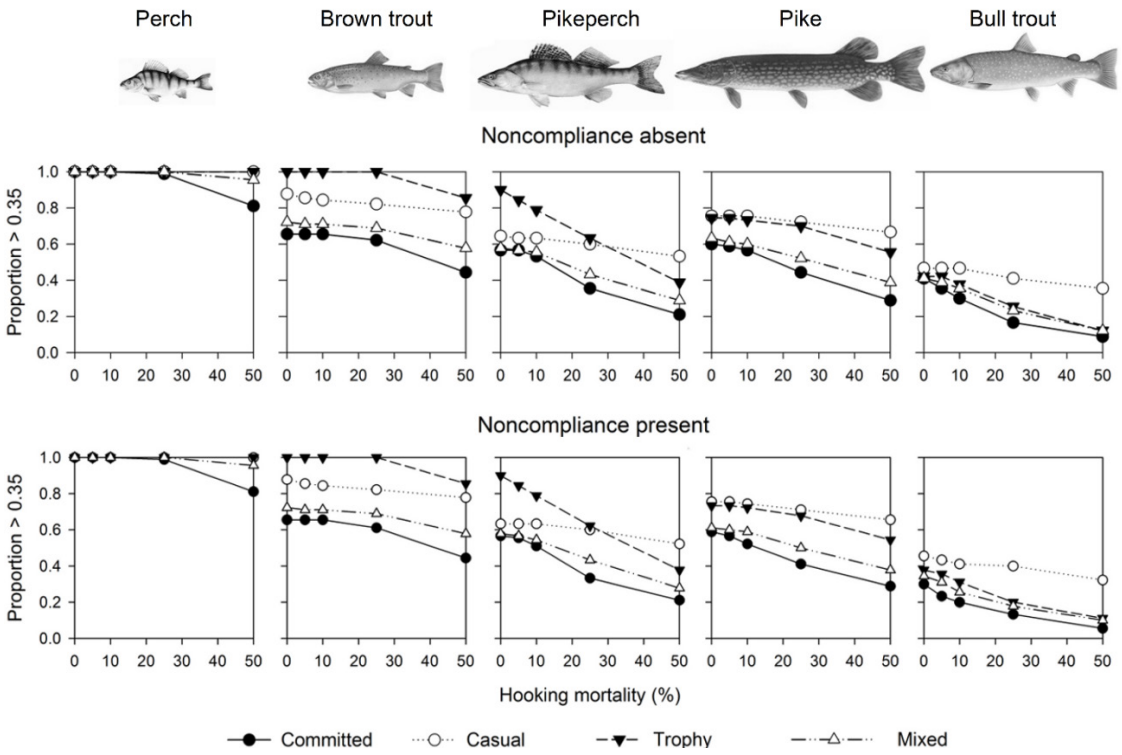


Figure 3. The proportion of simulations across the range of minimum-size limits and license numbers tested (excluding zero licenses) that resulted in a spawning-potential ratio > 0.35 under different levels of hooking mortality, in the presence and absence of noncompliance. Results are presented for the different angler populations and fish life-history types examined.

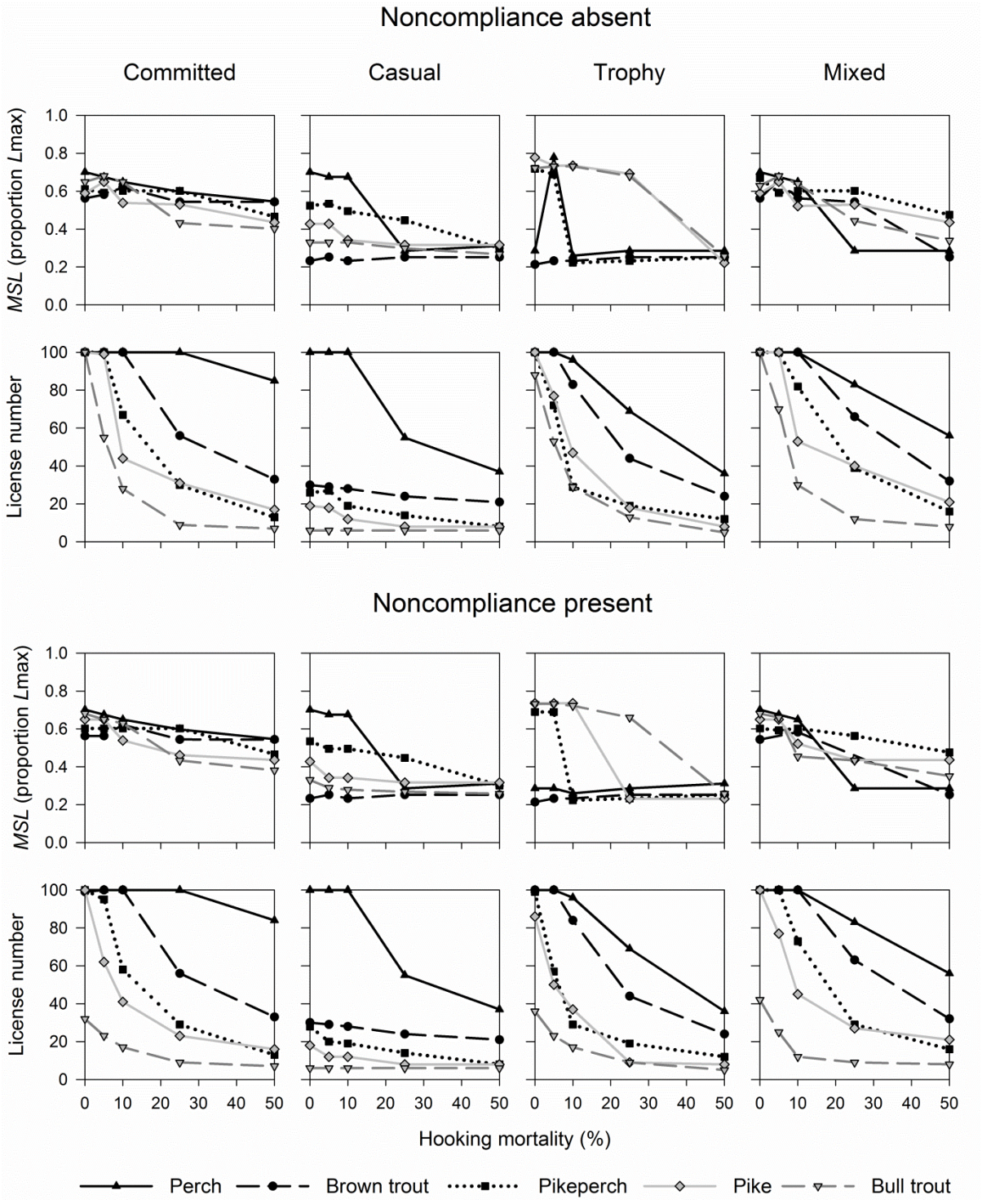


Figure 4. Optimal minimum-size limit (MSL, as a proportion of L_{max}), optimal license number, and spawning-potential ratio (SPR) under different levels of hooking mortality, in the presence and absence of noncompliance mortality. Results are presented for different angler populations and fish life-history types.

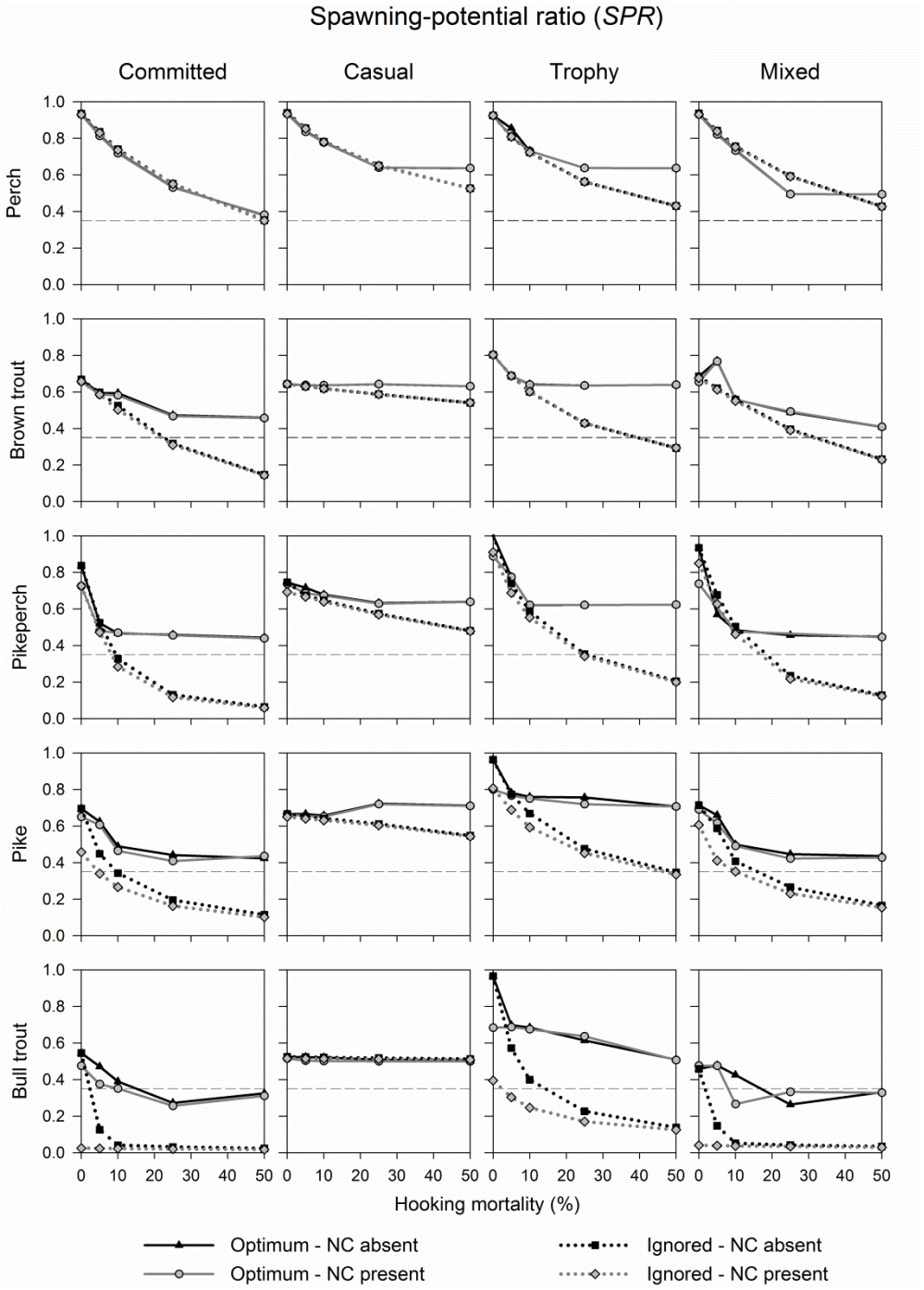


Figure 5. The influence of the presence (Sullivan-type relationship) and absence of noncompliance (NC) mortality, across a range of hooking mortality levels, on the spawning-potential ratio (SPR) that results under scenario optimal regulations (solid lines) and under the optimal regulations predicted when hooking mortality is ignored (i.e., 0% hooking mortality and no noncompliance; dotted lines). Results are presented for different angler populations and fish life-history types. The horizontal dashed line indicates a SPR of 0.35.

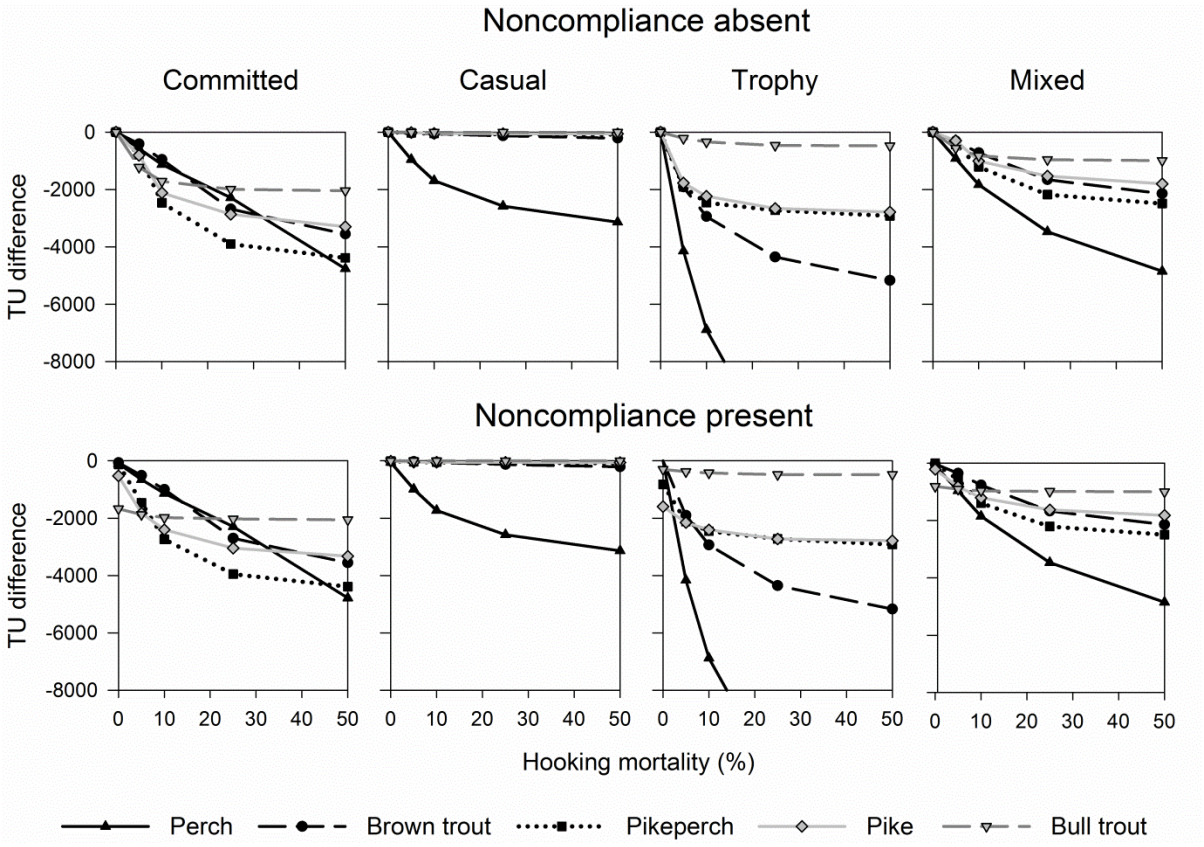


Figure 6. The change in total utility under optimal regulations at different levels of hooking mortality, in the presence and absence of noncompliance mortality. The difference presented is relative to the total utility when hooking mortality and noncompliance were absent. Results are presented for different angler populations, homogeneous and mixed, and for different fish life-history types.

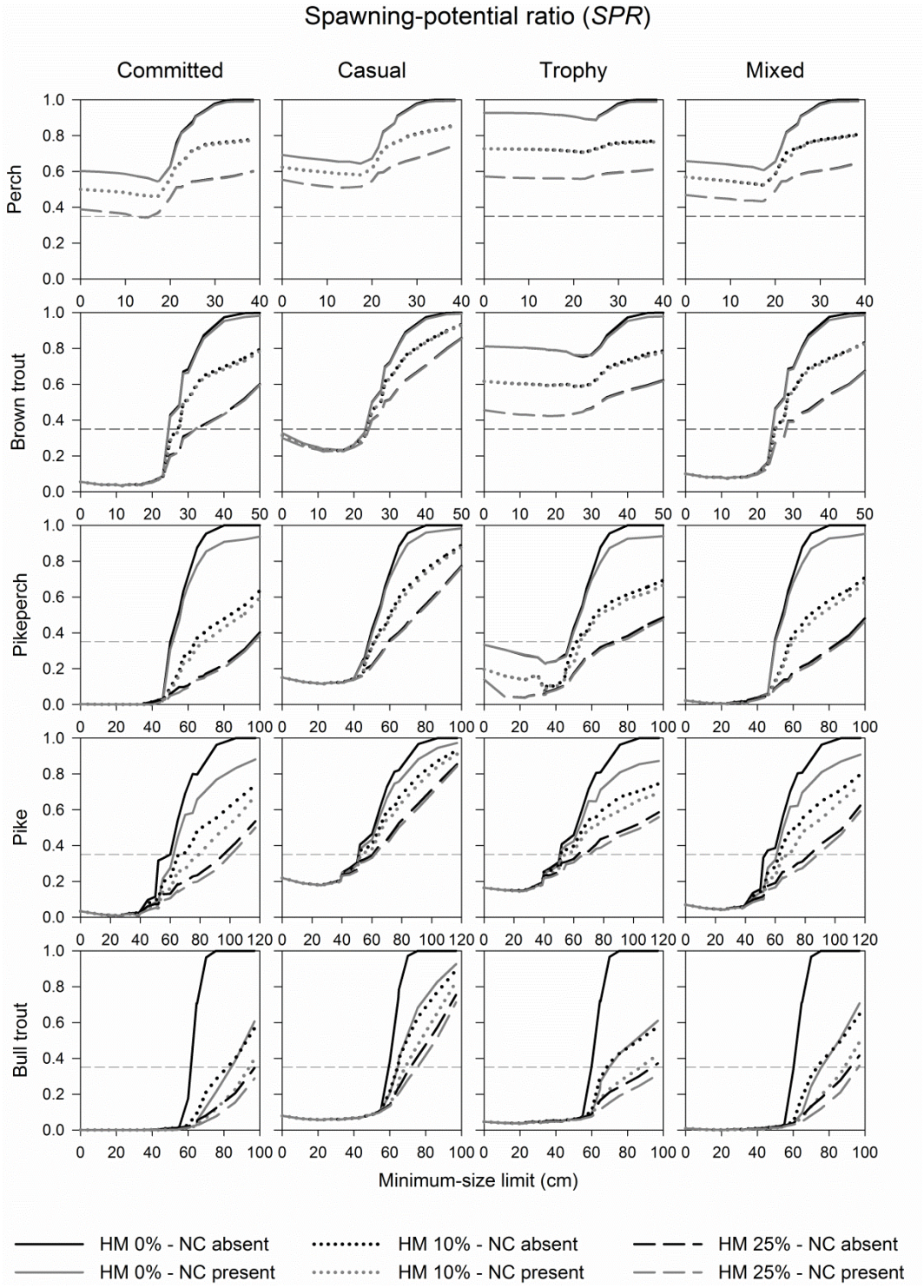


Figure 7. The biological consequences in terms of spawning-potential ratio (SPR) of hooking mortality (HM) in the presence and absence of noncompliance (NC) mortality when license numbers are maximized, mimicking an open-access fishery. Three levels of hooking mortality were examined, 0%, 10% and 25%.

APPENDIX

Part-worth utility functions adjustments: average daily catch, minimum-size limit, and daily bag limit

The part-worth utility (PWU) function for average daily catch presented by Beardmore et al. (2013) was altered to improve its use in the present model. The main reason justifying the change was that the range of catch rates tested by Beardmore et al. (2013) did not include extremely low catch levels, and the extreme nonlinearities that likely occur in this parameter space because anglers are very unlikely to fish on lakes where catch rates are zero (Cox et al. 2003). Using the original scale and functional form would substantially overestimate probability of angling when catch rates drop to very low levels in the model environment. Thus, we fitted a quadratic function through the predicted PWU at the four levels of catch rates tested by Beardmore et al. (2013) and two additional points that extend the PWU function beyond the levels tested in the choice experiment; one where catch rates were zero, and one at the maximum relative catch possible (see below). The PWU at the point of zero catch was set at the utility that would result in a probability of fishing of 6, 5, and 13% (committed, casual, and trophy anglers, respectively), when PWU of all other attributes equals zero, reflecting the average fishing experience for these other attributes, but accounting for differences in the intercept terms (i.e., the base alternatives of fishing outside the study area of Mecklenburg-Vorpommern, and not fishing at all, see Beardmore et al. 2013). The probability values used (6, 5, and 13%) correspond to the percentage of all trips taken by each angler type that were taken by anglers of that type who had average daily catch rates of zero (i.e., they never caught a fish on any trip) as reported in angler diaries when perch, pike or pikeperch were targeted (146/2401, 59/1117, 17/133, trips for class 1, class 2, and class 3 anglers, respectively). In addition, to minimize the likelihood that the PWU would decline at catch rates higher than those tested by Beardmore et al. (2013), we included the second additional point at the maximum standardized catch rate achieved under unexploited conditions. The PWU at this maximum point was predicted using the original linear coefficients from Beardmore et al. (2013) for daily catch.

To allow relative MSL and daily bag limits to be modelled as continuous variables, rather than as discrete function as in the original stated preference survey by Beardmore et al. (2013), quadratic functions were fit to the data. The means or current levels used to standardize these regulatory attributes in a manner similar to Beardmore et al. (2013) are provided in Table A3. In terms of daily bag limits, Beardmore et al. (2013) tested a wide range of attribute levels, so no additional data was required for the fit of the PWU function for this attribute. The only assumption made here was that unlimited bag limits were 3 times the average daily catch rate mean, as this is beyond the maximum catch rates possible in our model. MSL, however, was only tested at four levels over a narrower range in the choice experiment by Beardmore et al. (2013). Thus, while data was available for no MSL, extremely high values that result in mandatory catch-and-release (C&R) were not part of the stated preference survey. Thus, we added an additional point that represented mandatory C&R (e.g., $L_{\max}$) to the dataset used to fit the PWU function for MSL. The PWU at the point of mandatory C&R was set at the utility that would result in a probability of fishing of 5%, 10% and 20% for committed, casual, and trophy anglers respectively, when the PWU of all other attributes equaled zero, but accounting for differences in intercept terms (i.e., the base alternatives of fishing outside the study area, and not fishing at all). Differences in the aversion to restrictive MSLs (i.e., the use of 5%, 10% or 20%) among the angler types reflected differences in how important harvest and commitment to angling were for determining class membership as reported by Beardmore et al. (2013), and reflected differences in anglers' propensity to voluntarily release fish (Table A4). In terms of other fishing practices (e.g., skill/catchability, and gear type/vulnerability to capture) anglers were assumed to be identical.

Table A1. Bioeconomic model equations. Model variables are listed in Table A2. Parameter values and their sources for the fish life-history types studied here are listed in Table S1 of the supplementary material. Information for calculating part-worth utility (PWU) is given in Table A3. Parameters describing fishing practices of angler types and other relevant parameters can be found in Table A4.

	Equation	Description
	Individual-angler utility	
1	$U_{\mathrm{f}j} = U_{\mathrm{in}\,j} + U_{\bar{c}_{\mathrm{D}}j} + U_{\bar{l}j} + U_{l_{\max}j} + U_{\bar{A}_{\mathrm{D}}j} + U_{MSLj} + U_{DBLj} + U_{\mathrm{Dist}\,j} + U_{\mathrm{Cost}\,j} + U_{\mathrm{Stock}\,j} + U_{\mathrm{Spp}\,j}$	Conditional indirect utility gained by an angler of type j from choosing to fish (where $U_{\mathrm{in}\,j}$ is the basic utility gained from fishing, $U_{\bar{c}_{\mathrm{D}}j}$ is the PWU of average daily catch, $U_{\bar{l}\,j}$ is the PWU of average size of fish caught annually, $U_{l_{\max}j}$ is the PWU of maximum size of fish caught annually, $U_{\bar{A}_{\mathrm{D}}j}$ is the PWU of angler crowding, U_{MSLj} is the PWU of minimum-size limit, U_{DBLj} is the PWU of daily bag limit, $U_{\mathrm{Dist}\,j}$ is the PWU of distance, $U_{\mathrm{Cost}\,j}$ is the PWU of annual license cost, $U_{\mathrm{Stock}\,j}$ is the PWU of stock status, and $U_{\mathrm{Spp}\,j}$ is the PWU of effort to preferred species).
	Angler-effort dynamics	
2a	$p_{\mathrm{f}j} = \dfrac{4\exp(\hat{U}_{\mathrm{f}j})}{[4\exp(\hat{U}_{\mathrm{f}j}) + \exp(U_{\mathrm{out}}) + \exp(U_{\mathrm{no}})]}$	Probability an angler of type j chooses to fish, over the alternative to not fish (where $\hat{U}_{\mathrm{f}\hat{j}}$ applies to the previous year and U_{n} is the utility gained from not fishing)
2b	$p_{\mathrm{F}j} = (1-\varphi)p_{\mathrm{f}\hat{j}} + \varphi\hat{p}_{\mathrm{F}j}$	Realized probability an angler of type j fishes (where $\hat{p}_{\mathrm{F}j}$ applies to the previous year)
2c	$D_j = p_{\mathrm{F}j}D_{\max}$	Number of days an angler of type j chooses to fish during a year
2d	$A_{\mathrm{L}j} = \rho_j A_{\mathrm{L}}$	Density of licensed anglers of type j
2e	$E_j = D_j A_{\mathrm{L}j}\Psi$	Total annual realized fishing effort density by anglers of type j

2f	$e_{jt} = \begin{cases} E_j / S_{\mathrm{F}} & \text{if } t \le S_{\mathrm{F}} \\ 0 & \text{if } t > S_{\mathrm{F}} \end{cases}$	Instantaneous fishing effort density at time t by anglers of type j
	Age-structured fish population	
3a	$N_{\mathrm{total}} = \sum_{a=0}^{a_{\max}} N_a$	Total fish population density
3b	$B_{\mathrm{total}} = \sum_{a=0}^{a_{\max}} N_a W_a$	Total fish biomass density
	Growth	
4a	$h = h_{\max} / [1 + B_{\mathrm{total}} / B_{1/2}]$	Maximum annual growth of a fish dependent on the total fish biomass density at the beginning of the year
4b	$p_a = \begin{cases} 1 - \dfrac{G}{3+G}(1 + L_{a0}/h) & \text{if } a \ge a_{\mathrm{m}} - 1 \\ 1 & \text{if } a < a_{\mathrm{m}} - 1 \end{cases}$	Proportion of the growing season during which a fish of age a allocates energy to growth
4c	$g_{at} = \begin{cases} h / S_{\mathrm{G}} & \text{if } t \le p_a S_{\mathrm{G}} \\ 0 & \text{if } t > p_a S_{\mathrm{G}} \end{cases}$	Instantaneous growth rate in length of a fish of age a at time t
4d	$L_{at} = L_{a0} + g_{at} t$	Length of a fish of age a at time t
4e	$W_{at} = w L_{at}^{l}$	Mass of a fish of age a at time t
	Reproduction	
5a	$R_a = \begin{cases} \delta W_{at_{\mathrm{R}}} GSI / W_{\mathrm{e}} & \text{if } a \ge a_{\mathrm{m}} \\ 0 & \text{if } a < a_{\mathrm{m}} \end{cases}$	Annual fecundity of a female of age a given their mass at time t_R

5b	$b = \Phi \sum_{a=a_{\mathrm{m}}}^{a_{\max}} R_a N_a$	Annual population fecundity density (pulsed at the beginning of the year)
5c	Beverton-Holt: $s_0 = \alpha_{\mathrm{BH}} / (1 + \beta_{\mathrm{BH}} b)$ Ricker: $s_0 = \alpha_{\mathrm{R}} \exp(-\beta_{\mathrm{R}} b)$	Survival probability from spawning to post-hatch of fish of age 0 (applied at the beginning of the year)
5d	$N_0 = s_0 b$	Density of fish of age 0 at the beginning of the year
	Mortality	
6a	$v_{ajt} = \dfrac{1}{1 + \exp(-y(L_{at} - L_{50\,j}))}$	Proportion of fish of age a that are vulnerable to capture by anglers of type j at time t
6b	$L_{50} = z_j L_{\max} + L_{\mathrm{shift}}$	Size at 50% vulnerability to capture
6c	$c_{ajt} = q_j e_{jt} v_{ajt}$	Instantaneous per capita catch rate of fish of age a by anglers of type j at time t
6d	$H_{ajt} = \begin{cases} 1 & \text{if } L_{at} \geq MSL \\ f_{\mathrm{n}j} & \text{if } L_{at} < MSL \end{cases}$	Proportion of fish of age a that are harvestable by anglers of type j at time t
6e	$C_{jt} = \sum_{a=0}^{a_{\max}} c_{ajt} N_a H_{ajt}$	Instantaneous catch rate of fish that are harvestable by anglers of type j at time t
6f	$C_{\mathrm{H}jt} = \min(C_{jt}, c_{\max\,j} e_{jt} / \Psi, e_{jt} DBL / \Psi)$	Instantaneous harvest rate by anglers of type j at time t
6g	$f_{\mathrm{H}jt} = \dfrac{C_{\mathrm{H}jt}}{C_{jt}} + f_{\mathrm{h}j} \dfrac{C_{jt} - C_{\mathrm{H}jt}}{C_{jt}}$	Proportion of harvestable fish killed by anglers of type j at time t
6h	$m_{\mathrm{f}ajt} = f_{\mathrm{H}jt} c_{ajt} H_{ajt} + f_{\mathrm{h}j} c_{ajt} (1 - H_{ajt})$	Instantaneous per capita fishing mortality rate of fish of age a from anglers of type j at time t
6i	$d_{at} = m_{\mathrm{n}a} + \sum_j m_{\mathrm{f}ajt}$	Instantaneous per capita mortality rate of fish of age a at time t

6j	$\frac{dN_a}{dt} = -d_{at}N_a$	Instantaneous rate of change in the density of fish of age a at time t
	Response variables	
7a	$SPR = b_F / b_U$	Spawning-potential ratio (= annual population fecundity density b_F under fishing relative to annual population fecundity density b_U under unfished conditions)
7b	$U_{TU} = \sum_j U_{fj} D_j A_{Lj}$	Annual total utility

Table A2. Model variables. Bioeconomic model equations are listed in Table A1 and parameters for life-history types are listed in Table S1. Parameters used to describe angler-type behaviour and fishing practices are specified in Tables A3 and A4, respectively.

Symbol	Description (unit, where applicable)	Value or range
Index variables		
t	Time within the year (y)	0.0 - 1.0
a	Age class (y)	0 - $a_{\max}$
j	Angler type	committed; casual; trophy
Angling regulations		
MSL	Minimum-size limit (cm)	0 - $L_{\max}$
A_{L}	Number of licenses issued	0 – 100
Angling practices		
$f_{\mathrm{h}j}$	Proportion of fish dying from hooking mortality	0.0, 0.05, 0.10, 0.25, 0.50
$f_{\mathrm{n}j}$	Proportion of fish under the legal size limit MSL harvested illegally	0; Sullivan equation
Age-structured fish population		
N_a	Density of fish of age a (ha^{-1})	0 - ∞
L_{a0}	Length of fish of age a at the beginning of a year (cm)	0 - $L_{\max}$

Table A3. Parameter values used to determine part-worth utility functions (PWU) for the angler-behaviour model. PWU of an attribute $PWU = \beta_0 + \beta_1 X + \beta_2 X^2$, where X is the value of the attribute.

Symbol	Attribute	Mean or current level* $(\bar{X})$	Coefficient of variation	Fixed level	Standardization	PWU Intercept or constant† β_0	PWU Linear coefficient† β_1	PWU Quadratic coefficient† β_2
$\bar{c}_{Dj}$	Average daily catch	14.40, 5.67, 2.20, 0.71, 0.26	0.29	n.a.	$(X - \bar{X})/\sigma$	-0.148, -0.103, -0.075‡	0.637, 0.506, 0.348‡	-0.127, -0.088, -0.064‡
$\bar{l}_j$	Average size caught (cm)	15, 22, 42, 47, 45	0.036	n.a.	$(X - \bar{X})/\sigma$	0,0,0	0.028, 0.181, 0.412	0,0,0
$l_{\max j}$	Maximum size caught (cm; 95th percentile)	21, 31, 63, 73, 69	0.043	n.a.	$(X - \bar{X})/\sigma$	0,0,0	0.114, 0.046, 0.106	0,0,0
$\bar{A}_D$	Average daily crowding	4.5, 4.5, 4.5, 3.4, 3.4	0.80	n.a.	$(X - \bar{X})/\sigma$	0,0,0	-0.072, -0.104, -0.132	0,0,0
MSL	Minimum-size limit (cm)	20, 22, 45, 50, 40	n.a.	n.a.	$X/\bar{X}$	-0.029, -0.026, -0.031 ‡	1.542, 1.336, 0.721 ‡	-1.245, -1.082, -0.571 ‡
DBL	Daily bag limit	Mean average daily catch	n.a.	3•Mean average daily catch	$X/\bar{X}$	-0.170, -0.331, -0.292 ‡	0.235, 0.449, 0.548 ‡	-0.056, -0.106, -0.164 ‡
Dist	Distance (km)	n.a.	n.a.	20	$X/20$	0,0,0	-0.105, -0.226, -0.085	0,0,0
Cost	Annual license fee (€)	n.a.	n.a.	50	$X/10$	0,0,0	-0.029, -0.118, -0.132	0,0,0
Stock	Stock status	n.a.	n.a.	No information	n.a.	0.095, 0.064, 0.011	0,0,0	0,0,0
Spp	Effort to preferred species	n.a.	n.a.	100%	n.a.	0.497, 0.412, 1.365	0,0,0	0,0,0
U_{inj}	Intercept – utility gained from fishing within M-V	n.a.	n.a.	n.a.	n.a.	0.790, -0.194, -0.578	0,0,0	0,0,0

$U_{\text{out}j}$	Utility gained from fishing outside of M-V	n.a.	n.a.	n.a.	n.a.	-0.286, -1.181, 1.074	0,0,0	0,0,0
$U_{\text{no}j}$	Utility gained from not fishing	n.a.	n.a.	n.a.	n.a.	-0.504, 1.376, -0.496	0,0,0	0,0,0

n.a., not applicable. *Where relevant values given for perch, brown trout, pikeperch, pike, and bull trout respectively. †Parameter values for PWU functions are given for committed, casual, and trophy anglers respectively, as reported by Beardmore et al. (2013) unless otherwise noted by ‡ symbol (see methods for description).

TABLE A4 Parameters describing the fishing practices of angler types, and other angler-type related parameters.

Symbol	Description	Value
y_j	Steepness of size-dependent vulnerability curve	0.36
z_j	Size as a proportion of $L_{\max}$ used when calculating the size at which 50% of the fish are vulnerable to capture L_{50}	0.18
q_j	Catchability – skill level (ha h^{-1})	0.020
$c_{\max j}$	Desired average daily harvest	4, 4, 0.5*
ρ_j	Proportion of the angler population composed of anglers of type j	0.58, 0.33, 0.09
φ	Persistence of fishing behaviour (= the relative influence of last year's realized fishing probability on the current year's realized fishing probability)	0.5
$D_{\max}$	Maximum number of days that an angler would fish per year irrespective of fishing quality	40
Ψ	Average time an angler will fish in a day (h)	4
S_F	Annual duration of the fishing season (y)	1.0
ϕ	Lake area (ha)	100

* Values for desired average daily harvest reflected the average number of fish kept per trip by angler classes (Beardmore, *Unpublished data*). There was often no MSL for perch on waterbodies in the study area. Thus, to avoid the issue that harvest of <100% of the fish captured could simply have been due to regulatory constraints, the average daily harvest (4 fish d^{-1}) of committed and casual anglers was assumed to reflect the average number of perch kept per trip (4.3 and 4.05, for committed and casual anglers respectively). While trophy anglers had a similar daily harvest of perch (4.1 fish d^{-1}), their retention rates of pike and pikeperch rarely exceeded 0.5 fish d^{-1} (80% and 100% ≤ 0.5 fish d^{-1}, for pike and pikeperch respectively) and were substantially lower than that of the other angler types (43% and 39% ≤ 0.5 fish d^{-1} for committed anglers, and 52% and 65% ≤ 0.5 fish d^{-1} for casual anglers, pike and pikeperch respectively), despite similar catch rates. Thus, given this result and to add contrast to our angler types in terms of propensity to voluntarily release fish, we assumed the average daily harvest of trophy anglers to be 0.5 fish d^{-1}.

Paper V

V

Gwinn, D. C., M. S. Allen, F. D. Johnston, P. Brown, C. R. Todd, and R. Arlinghaus. *In Press*. Rethinking length-based fisheries regulations: the value of protecting old and large fish with harvest slots. Fish and Fisheries. DOI: 10.1111/faf.12053.

FISH and FISHERIES

Rethinking length-based fisheries regulations: the value of protecting old and large fish with harvest slots

Daniel C Gwinn[1], *Micheal S Allen*[1], *Fiona D Johnston*[2,3], *Paul Brown*[4], *Charles R Todd*[5] & *Robert Arlinghaus*[2,3]

[1]Program for Fisheries and Aquatic Sciences, School of Forest Resources and Conservation, The University of Florida, Gainesville, FL, 32653-3071, USA; [2]Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587, Berlin, Germany; [3]Chair for Integrative Fisheries Management, Faculty of Agriculture and Horticulture, Humboldt-Universität zu Berlin, Philippstrasse 13, 10115, Berlin, Germany; [4]Department of Environment and Primary Industries, Management and Science Branch Fisheries Victoria, Queenscliff Centre, PO Box 114, Queenscliff, Vic., 3225, Australia; [5]Department of Environment and Primary Industries, Arthur Rylah Institute for Environmental Research, 123 Brown Street, Heidelberg, Vic., 3084, Australia

Abstract

Managing fisheries using length-based harvest regulations is common, but such policies often create trade-offs among conservation (e.g. maintaining natural age-structure or spawning stock biomass) and fishery objectives (e.g. maximizing yield or harvest numbers). By focusing harvest on the larger (older) fish, minimum-length limits are thought to maximize biomass yield, but at the potential cost of severe age and size truncation at high fishing mortality. Harvest-slot-length limits (harvest slots) restrict harvest to intermediate lengths (ages), which may contribute to maintaining high harvest numbers and a more natural age-structure. However, an evaluation of minimum-length limits vs. harvest slots for jointly meeting fisheries and conservation objectives across a range of fish life-history strategies is currently lacking. We present a general age- and size-structured population model calibrated to several recreationally important fish species. Harvest slots and minimum-length limits were both effective at compromising between yield, numbers harvested and catch of trophy fish while conserving reproductive biomass. However, harvest slots consistently produced greater numbers of fish harvested and greater catches of trophy fish while conserving reproductive biomass and a more natural population age-structure. Additionally, harvest slots resulted in less waste in the presence of hooking mortality. Our results held across a range of exploitation rates, life-history strategies and fisheries objectives. Overall, we found harvest slots to represent a valuable option to meet both conservation and recreational fisheries objectives. Given the ubiquitous benefits of harvest slots across all life histories modelled, rethinking the widespread use of minimum-length limits is warranted.

Keywords Conservation, longevity overfishing, minimum-size limit, multiple objectives, open slot, recreational fishing, trade-offs

Correspondence:
Daniel C Gwinn,
Fisheries and Aquatic Science Program,
School of Forest Resources and Conservation,
University of Florida,
7922 North West 71st Street,
Gainesville, FL 32653-3071, USA
Tel.: 352-273-3624
Fax: 352-392-3672
E-mail: dgwinn@ufl.edu

Received 18 Jun 2012
Accepted 1 Aug 2013

DOI: 10.1111/faf.12053

Introduction

Recreational fishing constitutes the main use of freshwater fish stocks, and many coastal ones, in all industrialized and many developing nations (Arlinghaus *et al.* 2002a; FAO 2012). To protect fish stocks from overfishing and meet ecological and social objectives, length-based management is common (Radomski *et al.* 2001; Lewin *et al.* 2006). Simple harvest regulations were already in use in mediaeval times (Redmond 1986; Welcomme 2001; Arlinghaus *et al.* 2002b), and they are widely used in freshwater recreational fisheries (Noble and Jones 1999; Paukert *et al.* 2001; Radomski *et al.* 2001). As the recreational use of fish populations in coastal zones increases (Coleman *et al.* 2004; Pawson *et al.* 2008; Ihde *et al.* 2011; Lloret and Font 2013), length-based management will likely become more prevalent in many saltwater fisheries as well (Van Poorten *et al.* 2013).

Length-based harvest regulations help achieve the maximum sustainable yield (MSY) and may contribute to the optimum social yield (OSY) in recreational fisheries (Roedel 1975; Hudgins and Malvestuto 1996). MSY was a relevant objective in recreational-fisheries management in times when subsistence motives were common (Redmond 1986; Nielsen 1999). However, consumptive motives are on the decline in many recreational fisheries (Arlinghaus *et al.* 2007; Allen *et al.* 2008; Myers *et al.* 2008). Correspondingly, the key management objective is no longer biomass-based MSY, but optimizing the quality of a multifaceted fishing experience to anglers (Crutchfield 1962; Hendee 1974; Roedel 1975; Driver 1985; Johnston *et al.* 2010).

Many factors contribute to the quality of fishing as perceived by anglers (Freudenberg and Arlinghaus 2010), and both catch-related and non-catch-related attributes of the fishing experience play a role (Hunt 2005). Although variation among cultures and fisheries exist (Bryan 1977; Fisher 1997; Dorow *et al.* 2010), non-harvest attributes of the catch-related fishing experience, such as catch rate (Anderson 1993; Cox *et al.* 2003) and size of the fish captured (Powers *et al.* 1975; Jacobson 1996; Arlinghaus 2006), are important for angler utility and satisfaction. The quality of a recreational fishery may thus be maximized at lower fishing mortality than the fishing mortality that produces MSY (Caddy 1999; Radomski *et al.* 2001). This occurs because at low fishing mortality, the degree of size and age truncation is less pronounced, in turn potentially achieving a compromise between modest harvest and improving the potential for anglers to catch large, trophy fish. Hilborn (2007) called this area left to the MSY on an inverted dome-shaped yield curve a 'zone of new consensus' because it may satisfy the interests of multiple stakeholders better than a biomass-based MSY objective.

At high fishing effort levels, length-based harvest limits are needed to prevent overfishing and meet management objectives. The most common technique is a minimum-length limit (MLL), where small, usually immature fish must be released and fish over the MLL may be harvested. Other length-based harvest regulations include maximum-length limits and combinations of minimum- and maximum-size limits that result in either harvest-slot limits (harvest of intermediate size fish, also referred to as harvest window, inverse slot or open slot) or protected slot limits (where intermediate size classes are protected from harvest) (Noble and Jones 1999; FAO 2012).[1] The majority of research on slot limits has been devoted to protected slots (e.g. Wilde 1997; Pierce and Tomcko 1998; Dotson *et al.* 2013), with no empirical assessment published on the performance of harvest slots. Despite this lack of research, harvest slots (HSs) are in use in selected fisheries such as some

[1]Note that the unqualified term 'slot limit' should not be used to avoid confusion; it is used interchangeably in the literature to mean either open or closed slot.

Florida inshore fish stocks in the Gulf of Mexico, the sturgeon fisheries on the west coast of North America and Nile perch (*Lates niloticus*, Latidae) in Lake Victoria (Law *et al.* 2012).

Some theoretical studies on the effectiveness of HSs have been conducted, but they were focused on a species-specific level (Arlinghaus *et al.* 2010 for northern pike *Esox lucius*, Esocidae, Clark *et al.* 1980; Jensen 1981; García-Asorey *et al.* 2011 for various freshwater salmonids including the anadromous steelhead *Oncorhynchus mykiss*, Salmonidae, and Koehn and Todd 2012 for Murray cod, *Maccullochella peelii*, Percichthyidae). Few generic fish population models have examined the performance of HSs, relative to alternative harvest regulations (Reed 1980; Botsford and Hobbs 1986; Law *et al.* 2012). Moreover, all these studies were strictly focused on optimizing biomass yield, and no research has compared the relative performance of HSs versus the more common MLLs across a range of fish life histories against alternative objectives to biomass yield, such as maximizing harvest numbers and the abundance of trophy fish.

The purpose of this study was to identify outcomes and trade-offs when applying HSs and MLLs to provide numerical harvest (harvest), biomass harvest (yield), trophy catch and stock conservation (using a range of indices). We performed this evaluation using a general age- and size-structured model for two prototypical fish populations that represented two extreme forms of productivities (life history). To provide a broad context to our results, we also evaluated the utility of HSs for managing several recreationally important fish species characterized by more specific life histories. The results have broad implications by calling into question the almost 'default' use of MLLs to manage recreational fisheries around the globe.

Conceptual background and review of length-based harvest regulations

The rationale for length-based harvest regulations involves at least four concerns. First, size limits are designed to avoid recruitment overfishing (Allen *et al.* 2013). Such arguments are common in the implementation of the popular MLLs based on the 'spawn-at-least-once' idea (Novinger 1984; Redmond 1986). Second, length-based harvest limits are intended to manage the size-structure of fish stocks to meet expectations of anglers (Clark *et al.* 1980; Jensen 1981; Noble and Jones 1999). Third, directing exploitation on particular size-classes can produce the MSY. Many age-structured models developed in the mid-20th century predicted an optimal age at entry into the fishery to maximize biomass yield (Ricker 1945; Allen 1953; Saila 1956; Beverton and Holt 1957). Because age and size are correlated and due to the impossibility to harvest single age classes entirely, these findings were transferred into management practice by implementing a MLL where over this size aggressive culling would maximize biomass yield or yield per recruit (Dunning *et al.* 1982; Maceina *et al.* 1998). A final reason for length-based harvest limits is convenience. Recreational fisheries are often open access, and there is a paucity of monitoring information for more complex management across the fisheries landscape (Post *et al.* 2002). In the absence of fishery-specific information, implementation of a MLL might be seen as a simple regulation intended to protect all stocks from recruitment overfishing. Correspondingly, in some countries, such as Germany, entire landscapes of spatially structured fisheries are commonly managed with one-size-fits-all MLLs (Daedlow *et al.* 2011). However, when fishing effort is intensive, a MLL severely truncates the size- and age-structure (Wilde 1997; Arlinghaus *et al.* 2010; Pierce 2010), which can affect the overall quality of the fishery by reducing the availability of trophy fish to anglers (Jacobson 1996; García-Asorey *et al.* 2011).

From a conservation perspective, there is renewed concern that the systematic removal of large fish may have ramifications for population fecundity and recruitment dynamics (e.g. Grey and Law 1987; Berkeley *et al.* 2004a,b; Birkeland and Dayton 2005). Several mechanisms have been proposed to explain why fisheries-induced demographic changes towards younger and smaller fish affect recruitment dynamics and productivity of stocks. First, a large fraction of young spawners amplifies a stock's non-linear dynamics, hence destabilizing its abundance (Reed 1983; Anderson *et al.* 2008; Hsieh *et al.* 2010). Second, in many fish species, spawning occurs at different times and areas for fish of different size/age (Wright and Trippel 2009), providing a buffer against environmental stochasticity (Berkeley *et al.* 2004a; Hidalgo *et al.* 2011; Rouyer *et al.* 2011). Third, the existence of age- and size-dependent maternal

effects on egg and larval quality could influence recruitment in some fish species (Berkeley *et al.* 2004a,b; Arlinghaus *et al.* 2010; Venturelli *et al.* 2010), but there is no agreement as to how prevalent this effect is in nature (O'Farrell and Botsford 2006; Marshall *et al.* 2010; Ottersen *et al.* 2013). Finally, in most fishes, fecundity increases exponentially with length and linearly with body mass (Wootton 1998). This is due to large fish not only having a greater body volume for holding eggs, but also because they may devote a greater fraction of surplus energy to egg production than smaller mature fish (Lester *et al.* 2004; Edeline *et al.* 2007). Thus, large fish have a greater relative reproductive value (Grey and Law 1987; Xu *et al.* 2013) and may contribute strongly to year class strength and surplus production under exploited conditions (Walters *et al.* 2008; Arlinghaus *et al.* 2010). Using length-based HSs to maintain highly fecund large individuals could thus represent a powerful strategy for managing fisheries sustainably.

The ultimate choice of the particular length-based harvest regulation depends on a range of factors such as management objective, population status, fishing mortality rate and the particular processes that govern a fish stock (FAO 2012). When the management objective is MSY, MLLs should be most useful when natural mortality and recruitment rates are low, and growth of fish is rapid (Novinger 1984; Brousseau and Armstrong 1987; FAO 2012). However, if size-related maternal effects influence recruitment (e.g. the fecundity reserve of large spawners; Venturelli *et al.* 2009, 2010), harvest-slot limits that protect both young and old fish might outperform MLLs over a range of fishing rates (Reed 1980; Arlinghaus *et al.* 2010; FAO 2012). Protected slots may perform better if people enjoy harvesting large fish, but for them to be effective recruitment must be sufficiently high (Brousseau and Armstrong 1987; FAO 2012). Protected slots are particularly advisable if competition among juvenile fish is excessive such that thinning of juvenile fish promises to relax competition, increase growth and reduce natural mortality (Brousseau and Armstrong 1987). For protected slots to work, however, people must be able and willing to harvest small fish (FAO 2012), which is often not the case (Wilde 1997; Pierce and Tomcko 1998). Thus, the applicability of protected slots may be less than for HSs and MLLs. This article therefore focused on HSs and MLLs for their utility in recreational fisheries management.

Despite the frequent use of length-based harvest limits in recreational fisheries (Radomski *et al.* 2001), most studies evaluating the effectiveness of such regulations are single-system case-studies that lack control fisheries and long time series and hence have low power to detect regulation effects (Allen and Pine 2000). In a meta-analysis, Wilde (1997) analysed MLLs and protected slots in largemouth bass (*Micropterus salmoides*, Centrachidae) fisheries in the U.S.A. He reported protected slots to be effective in increasing the proportion of large fish in the stock. However, the same regulations failed to increase angler catch rates, which is an indication that they did not elevate stock sizes. Additionally, MLLs failed to increase the proportion of large fish harvested by anglers (Wilde 1997). Based on these results and other considerations, some have questioned the usefulness of MLLs (Tesch and Wehrmann 1982; Conover and Munch 2002; Birkeland and Dayton 2005), and increasingly alternative regulations to MLLs are sought, in particular when maintaining large fish in the stock is considered important (Pierce 2010). In this context, the use of HSs has increasingly been proposed as alternative to MLLs to protect large and old as well as immature fish for reaping ecological (Berkeley *et al.* 2004a; Arlinghaus *et al.* 2010; Venturelli *et al.* 2010; Law *et al.* 2012), evolutionary (Conover and Munch 2002; Law 2007; Matsumura *et al.* 2011) and fisheries benefits (Jensen 1981; Arlinghaus *et al.* 2010). However, no theoretical research has tested the performance of HSs for a range of fish life histories relative to the much more widespread MLLs.

The model

We constructed an age- and size-structured population model to determine 'optimal' length-based fishery regulations when management objectives are to jointly consider several fishery attributes of value to anglers (harvest, yield and trophy catch), while conserving the fish stock's reproductive capacity and minimizing age and size truncation. To evaluate the performance of MLLs and HSs as fishery regulations across life histories, the model first simulated fish populations with low-productive and high-productive life histories that differed in longevity, growth and recruitment compensation levels (Myers *et al.* 1999; Goodwin *et al.*

2006). In the simulations, we accounted for natural mortality, harvest mortality, discard mortality (known in recreational fisheries as hooking mortality), length-based vulnerabilities to the fishery and density-dependent compensation in the recruitment process. We evaluated the fishery performance and conservation status for each life-history strategy, for medium and high exploitation scenarios, and across a range of MLLs and HSs to reveal regulations that provide a compromise among conservation and fishery objectives. We then modelled a series of specific fish species that commonly support recreational fisheries to provide context to our results and serve as a form of sensitivity analysis.

Model formulation

We simulated an age- and size-structured fish population with multiple growth trajectories similar in structure to Coggins *et al.* (2007). The model incorporated multiple growth trajectories to more realistically represent the effects of size-selective exploitation. The length-at-age of fish in each growth trajectory was modelled with a standard von Bertalanffy (1938) growth curve as:

$$L_{a,g} = L_{\infty,g}\left(1 - e^{-k(a-t_0)}\right), \qquad (1)$$

where $L_{a,g}$ is the total length of an age a (a = 1 to A) fish in growth trajectory g (g = 1 to G), k is the metabolic parameter that determines the rate that fish attain maximum length, t_0 is the theoretical age at length zero, and $L_{\infty,g}$ represents the maximum length of fish in growth trajectory g. We simulated variability in growth by assigning each growth trajectory a unique maximum length ($L_{\infty,g}$).

Equilibrium abundance at age for each growth trajectory ($N_{a,g}$) was calculated as the product of the predicted number of age-1 recruits at equilibrium (R_{eq}) and the proportion of fish surviving to each age ($l_{a,g}$) as

$$N_{a,g} = R_{eq} l_{a,g} p_g, \qquad (2)$$

where p_g is the probability of a fish belonging to a given growth trajectory. The parameter $l_{a,g}$ is the survivorship schedule that simulates the proportion of age-1 recruits surviving to each age for each growth trajectory. Survivorship to age a was calculated recursively for each growth trajectory as

$$l_{a,g} = l_{a-1,g} e^{-Z_{a,g}} \quad l_{1,g} = 1, \qquad (3)$$

where $Z_{a,g}$ is the total instantaneous mortality rate for age a in growth trajectory g. The total annual instantaneous mortality rate incorporated natural mortality, harvest mortality and discard mortality as

$$Z_{a,g} = M + FV_{a,g} + (F'V_{a,g} - FV_{a,g})D, \qquad (4)$$

where M is the instantaneous annual natural mortality rate, F and F' are the instantaneous annual harvest (i.e. exploitation) and catch rate of vulnerable fish, respectively, and $V_{a,g}$ and $V'_{a,g}$ are the length-specific vulnerabilities to harvest and catch, respectively. The parameter D is the discard mortality rate, which represents the proportion of caught and released fish that die due to the capture and handling process. Formulating the total mortality equation with instantaneous rates models a fishery where exploitation occurs continuously throughout each year and accounts for the competing risks of deaths due to exploitation, discard mortality and natural mortality. The vulnerability to harvest for a given age and growth trajectory ($V_{a,g}$) was expressed as a Boolean variable, where $V_{a,g}$ = 1 indicates that fish at age a in growth trajectory g are vulnerable to harvest and $V_{a,g}$ = 0 indicates that they are invulnerable to harvest. Thus, the values of $V_{a,g}$ were determined with a logical test to indicate vulnerability to the fishery as

$$\begin{aligned} &V_{a,g} = 1, \text{ when } L_{\min} < L_{a,g} < L_{\max}, \\ &V_{a,g} = 0, \text{ when } L_{\min} > L_{a,g} \text{ or } L_{\max} < L_{a,g}, \end{aligned} \qquad (5)$$

where L_{min} is the minimum length where fish are vulnerable to harvest and L_{max} is the maximum length where fish are vulnerable to harvest. Thus, L_{min} and L_{max} represent the lower and upper length limit of a HS, respectively, and simulated a cohort of fish gradually becoming vulnerable to the fishery as fish in each growth trajectory grow into the legal length range for harvest. The parameter $V'_{a,g}$ is the length-based vulnerability of fish to capture, which was also determined as a Boolean variable that took the value of one when $L_{a,g}$ was greater than the minimum length vulnerable to capture (L_{cap}) and was otherwise zero.

Equilibrium recruitment R_{eq} was predicted using a Botsford modification of a Beverton and Holt (1957) stock-recruitment function (Botsford 1981a,b). This formulation predicts the number of age-1 recruits of an exploited population at

equilibrium directly and is summarized in Walters and Martell (2004) as

$$R_{eq} = R_0 \frac{CR - (\Phi_0/\Phi_f)}{CR - 1}, \quad (6)$$

where R_0 is the number of age 1 recruits in the unfished condition and CR is the Goodyear recruitment compensation ratio (Goodyear 1980), which represents the maximum increase in juvenile survival at reduced densities. The parameters Φ_0 and Φ_f are fecundity incidence functions that account for the cumulative effects of natural mortality, harvest mortality and discard mortality on the total annual fecundity of the population in the unfished and fished condition, respectively. We calculated the fecundity incidence functions per Walters and Martell (2004) as

$$\Phi = \sum_g \sum_a p_g f_{a,g} l_{a,g}, \quad (7)$$

where $f_{a,g}$ is the average fecundity of fish of age a in growth trajectory g. Fecundity at age ($f_{a,g}$) was approximated as the difference between the mean weight-at-age and the weight-at-maturation because fecundity is usually directly proportional to weight (Walters and Martell 2004). When the mean weight-at-age was less than the weight-at-maturation, $f_{a,g}$ was set to a value of zero. This essentially modelled a 'knife-edge' transition of fish from immature to mature stages at the specified length at maturation. Weight-at-age was predicted using a standard length–weight relationship as

$$W_{a,g} = \alpha L_{a,g}^{\beta}, \quad (8)$$

where α is the scaling parameter and β is the allometric parameter that modifies the relationship between length and weight.

Model outputs

The model was used to evaluate three standardized (scaled) measures of fishery performance at equilibrium, (i) the proportion of the maximum possible number of fish harvested (hereafter referred to as harvest); (ii) the proportion of the maximum possible number of trophy fish caught; and (iii) the proportion of maximum possible biomass yield (hereafter referred to as yield). These metrics were chosen as indicators of the social and economic value of the fishery because they are common components of the fishing experience that anglers, managers or other stakeholders value (Jensen 1981; Jacobson 1996; Arlinghaus 2006). We present all metrics on a normalized scale as proportions of total possible to allow unambiguous comparisons and elucidate possible trade-offs.

The proportion of the maximum possible harvest (H) was calculated as

$$H = \frac{\sum_g \sum_a N_{a,g}(1 - e^{-FV_{a,g}})}{H_{\max}}, \quad (9)$$

where the term $(1 - e^{-FV_{a,g}})$ represents the proportion of age a fish harvested from each growth trajectory and $H_{\max}$ represents the maximum possible numbers harvested across the full range of both HS and MLL regulations for a given life-history/exploitation-rate scenario. Thus, the harvest obtained from each HS and MLL was compared with the maximum harvest value $H_{\max}$ obtained from any regulation.

Similarly, the proportion of the maximum possible number of trophy-sized fish caught by anglers (T) was calculated as

$$T = \frac{\sum_g \sum_a N_{a,g}\left(1 - e^{-FV'_{a,g}}\right) t_{a,g}}{T_{\max}}, \quad (10)$$

where $t_{a,g}$ was a Boolean variable that takes the value of one when $L_{a,g}$ was greater than or equal to trophy size fish and the value of zero when $L_{a,g}$ was less than a trophy size fish. Fish were considered trophy size if they were ≥85% of the average maximum total length across growth trajectories ($\overline{L}_{\infty}$). The parameter $T_{\max}$ represented the maximum possible numbers of trophy fish caught across the full range of both HS and MLL regulations for a given life-history/exploitation-rate scenario.

The proportion of maximum possible biomass harvested (yield) was calculated as

$$Y = \frac{\sum_g \sum_a N_{a,g} W_{a,g}(1 - e^{-FV_{a,g}})}{Y_{\max}}, \quad (11)$$

where $W_{a,g}$ is the weight of a fish at age a in growth trajectory g calculated with equation 8 and $Y_{\max}$ is the maximum possible yield across the full range of HS and MLL regulations for a given life-history/exploitation-rate scenario.

For simulations that included discard mortality, we calculated the harvesting efficiency (E) as a fourth performance metric. The E metric indicates the fraction of total fishery-related deaths that are due to harvest (Coggins *et al.* 2007; Arlinghaus *et al.* 2010). It was calculated as

$$E = \sum_g \sum_a \frac{N_{a,g}(1 - e^{-FV_{a,g}})}{N_{a,g}\left(1 - e^{-(Z_{a,g}-M)}\right)}, \qquad (12)$$

where the numerator is the number of harvested fish and the denominator is the total number of fishery-related mortalities (i.e. total mortalities – natural mortalities). Low values of E indicate a high proportion of fish deaths due to discard mortality after catch and release, and thus reduced harvesting efficiency.

We assessed the conservation status of all simulated life histories by calculating the spawning potential ratio (SPR) and a metric of juvenescence (J) due to fishery-induced age (and size) truncation of the stock. The SPR was applied as a measure of the reduction in per-recruit reproductive output of the fish populations and was calculated as the fecundity-per-recruit at equilibrium divided by the fecundity-per-recruit in the unfished condition (i.e. SPR = Φ_0/Φ_f). SPR is a common metric used to assess the sustainability of fisheries with values <0.35 indicating the potential for recruitment overfishing (Mace 1994; Allen *et al.* 2013). The J metric was used to index the alteration of the natural age- and size-structure and to account for the disproportional importance of old and large fish for recruitment and population stability (i.e. 'longevity overfishing', Beamish *et al.* 2006; Hsieh *et al.* 2010). The value of J was calculated as the total fecundity produced by the older half of the age classes divided by the total fecundity of the entire population ($R_{eq}\Phi_f$) at equilibrium. Thus, large J values indicated greater fecundity resulting from large, old fish, while small values indicated the loss of large fecund spawners in the population.

We defined three specific management objectives thought to be of relevance to recreational fisheries managers to evaluate the relative performance of HSs versus MLLs across the life-history types. The first objective was harvest-oriented management, the second objective was trophy catch-oriented management, and a third objective represents a compromise between harvest and trophy catch. To operationalize each objective, we drew on two normalized metrics of fishing quality, *viz*. the harvest numbers H and the catch of trophy fish T. We designed ratios between H and T to reflect underlying fishing qualities to be achieved for meeting a specific management objective. Accordingly, an objective that would aim at a ratio of the fishing quality H over T of 1.0 would reflect equal priority on both numbers of fish harvested and trophy catch. Meeting the ratio would represent identical fishing qualities for harvest and trophy catch as revealed by an identical percentage of H and T that would be present under the chosen regulation. Similarly, any ratio different from 1.0 would reflect an objective that aimed at producing a greater fishing quality on one of the two components, without entirely disregarding the other component. For illustrative purposes, we specified a harvest-oriented management objective as $H = 3T$, meaning that the harvest fishing quality H would be three times the fishing quality in terms of trophy catch T. Analogously, we defined a trophy-fish-catch-oriented management objective as one where the condition $3H = T$ is met, meaning that the fishing quality in terms of catch of trophy fish, T, would be three times that of the fishing quality for harvest H. Our compromise management objective was defined simply as $H = T$, resulting in an equal fishing quality of H and T. After identifying the specific regulation (either HS or MLL) that would meet the management objective, we calculated the fishery and conservation metrics at that regulation. Although the exact weighting of our management objectives is not likely to represent any management objective for a specific recreational fishery accurately, the specifications chosen provided a convenient reference for comparing the relative performance of MLLs and HSs for meeting conservation needs, while optimizing the fishing quality for a variety of exploited species.

Parameterization and outline of analysis

We expected that the efficacy of length-based regulations to optimize harvest, trophy catch and stock conservation would be influenced by the life-history characteristics of the fish and the level of exploitation applied by the fishery. Thus, we evaluated length-based regulations for two life-history strategies and two intensities of fishing (high and medium fishing mortality). The life-history strategies were parameterized to represent two extremes across a gradient of productivity levels, with one strategy representing a generic long-lived, low-productive species (LLLP) and the other strategy representing a generic short-lived, high-productive species (SLHP, Coggins *et al.* 2007). The LLLP represented a large-bodied fish with slow growth, late maturation and high levels of density-dependent

recruitment compensation (e.g. striped bass *Morone saxatilis*, Moronidae). The SLHP represented a smaller-bodied fish with fast growth, early maturation and low levels of density-dependent recruitment compensation (e.g. spotted seatrout *Cynoscion nebulosus*, Sciaenidae). Parameter values representing these life-history strategies were taken from Coggins *et al.* (2007) with some modifications (Table 1). The maximum age of the LLLP and the SLHP was set at 30 years and 10 years, respectively. Associated mortality and growth parameter values were then determined from life-history invariants. For example, the instantaneous natural mortality rate (M) was approximated from the maximum age as 0.15 per year for the LLLP and 0.44 per years for the SLHP using Hoenig (1983). The k parameter of the von Bertalanffy growth model was approximated from M as 0.1 for the LLLP and 0.29 for the SLHP using the established relationship of $M \approx 1.5\ k$ (Jensen 1996).

We simulated a total of 101 growth trajectories for each life-history type. Maximum length in each growth trajectory was assigned by first choosing a mean asymptotic length ($\overline{L}_\infty$) and then choosing a minimum ($L_{\infty,\min}$) and maximum ($L_{\infty,\max}$) value possible. The L_∞ of each growth trajectory was then assigned a value evenly spaced between $L_{\infty,\min}$ and $L_{\infty,\max}$. The mean asymptotic length ($\overline{L}_\infty$) of the LLLP and the SLHP was set at 1000 mm and 500 mm, respectively (Table 1). The values of the minimum ($L_{\infty,\min}$) and maximum ($L_{\infty,\max}$) asymptotic length were set as ±20% of $\overline{L}_\infty$ for both life-history strategies. This range approximated the 95% probability range of a normal distribution with a mean of $\overline{L}_\infty$ and a standard deviation of 10% of the mean. The proportion of the fish recruiting to each growth trajectory (p_g) was specified as the normal probability density of $L_{\infty,g}$ given a mean equal to $\overline{L}_\infty$ and a standard deviation of 10% of $\overline{L}_\infty$. This formulation of growth trajectories and p_g mimicked common variability in growth of exploited fish populations (Walters and Martell 2004).

We simulated a medium and high exploitation fishery on each life-history strategy. The medium exploitation fishery was specified by setting the instantaneous annual harvest rate (F) to 80% of the natural mortality. This approximates a fishery harvested near MSY (Walters and Martell 2004). The high exploitation fishery was specified by setting F to twice the natural mortality rate. Exploitation rates of this level generally cause growth and recruitment overfishing indicated by yields that are less than MSY (Walters and Martell 2004). For simplicity, we assumed that there was no voluntary release of fish by anglers (i.e. $F' = F$) and that discard mortality (D) was negligible for the base simulations. However, we evaluated fishery performance and stock conservation at two levels of discard mortality rates (D = 10 and 30%) in an additional sensitivity analysis because Coggins *et al.* (2007) noted that benefits of harvest regulations are tightly related to the level of

Table 1 Parameter input values provided for a long-lived low-productive (LLLP) and short-lived, high-productive (SLHP) life-history prototype.

Parameter	Description	LLLP	SLHP
R_0	Average age 1 recruitment in the unfished state	1 000 000	1 000 000
A	Maximum age (years)	30	10
M	Natural mortality rate (per year)	0.15	0.44
CR	Compensation ratio	25	5
$\overline{L}_\infty$	Average asymptotic length (mm)	1000	500
$L_{\infty,\min}$	Minimum asymptotic length (mm)	800	400
$L_{\infty,\max}$	Maximum asymptotic length (mm)	1200	600
k	von Bertalanffy growth coefficient (years)	0.1	0.35
t_0	Theoretical age at length zero (years)	0	0
L_{mat}	Length-at-maturation (mm)	400	200
α	Length–weight constant	3.5×10^{-5}	3.5×10^{-5}
β	Allometric parameter	2.8	2.8
L_{min}	Minimum length vulnerable to harvest (mm)	400	200
L_{cap}	Minimum length vulnerable to capture (mm)	250	125
L_{troph}	Minimum total length of a trophy fish (mm)	800	400

discard mortality. The discard mortality rate of 10% was chosen because it approximates a common hooking mortality rate that represents many recreational fisheries (Bartholomew and Bohnsack 2005; Hühn and Arlinghaus 2011), while the value of 30% was chosen because it generally exceeds the rate for which fishery sustainability can be achieved through length-based harvest regulations when F is high (Coggins *et al.* 2007).

We evaluated the performance of a range of MLLs and HSs by manipulating the vulnerability to harvest (Equation 5). We considered MLLs ranging from the length-at-maturation (L_{mat}) to the maximum length possible ($L_{\infty,\max}$). A MLL equal to L_{mat} modelled a fishery where all mature fish were legal to harvest, whereas a MLL equal to $L_{\infty,\max}$ modelled a total catch-and-release fishery. Similarly, we considered HSs with a minimum legal length (L_{min}) of L_{mat} and a maximum legal length (L_{max}) ranging from L_{mat} to $L_{\infty,\max}$. A HS with L_{max} equal to $L_{\infty,\max}$ modelled a fishery where all mature fish were legal to harvest, whereas L_{max} equal to L_{mat} modelled a total catch-and-release fishery. For the base simulations, we did not consider any regulation that allowed harvest of fish shorter than length-at-maturation because harvesting fish before they reach maturity significantly increases the risk of overfishing (Myers and Mertz 1998; Froese 2004) and is usually not implemented as a recreational-fisheries regulation. We fixed the lower length vulnerable to capture (L_{cap}) at 25% of $\overline{L}_{\infty}$ to provide a realistic standard across life-history strategies and because very small fish are usually not vulnerable to recreational fishing gear (Pierce *et al.* 1995; but see Alós *et al.* 2009).

To explore how our results would transfer to specific freshwater fish species commonly targeted by recreational anglers, we evaluated MLLs and HSs for Murray cod, lake trout (*Salvelinus namaycush*, Salmonidae), Eurasian perch (*Perca fluviatilis*, Percidae), arctic grayling (*Thymallus arcticus*, Salmonidae), zander (*Sander lucioperca*, Percidae) and northern pike. Murray cod and lake trout were chosen because these species have life-history characteristics that resemble the LLLP, and Eurasian perch was chosen because its life-history characteristics resemble the SLHP. Zander, northern pike and Arctic grayling were chosen because they represent fish species that do not easily correspond to the LLLP or the SLHP prototype and represent intermediate life-history strategies. All species chosen are valued for recreational fishing with both trophy and consumption components, although cultural differences exist (e.g. pike are usually consumed by anglers in Germany and often released voluntarily in the USA). Input parameter values for each species were taken from the literature or approximated from life-history invariants (Hoenig 1983; Jensen 1996; Table 2). The Goodyear recruitment compensation parameter (CR) was taken from Myers *et al.* (1999); when species-specific values were not available, we used the average for the taxonomic family.

Fisheries managers never have perfect information about critical life-history or fishery parameters required to set appropriate regulations. Hence, identifying regulations that are robust to incorrect knowledge about the fishery is important (Walters and Martell 2004). To evaluate the relative performance of HSs and MLLs in the face of parameter uncertainty, we performed a two-step sensitivity analysis. In the first step, we determined the regulation that met the management objectives with incorrect parameter input values (mimicking the determination of regulations with imperfect knowledge). In the second step, we applied the regulations determined with incorrect parameter inputs to the simulated fishery to determine how robust the regulation performance is to the incorrect parameter inputs. Using this approach, we evaluated uncertainty about the instantaneous natural mortality rate M, the recruitment compensation ratio CR, the length at maturation L_{mat} and the instantaneous fishery exploitation rate F. These four parameters were selected because they are important determinants of the productivity of stocks and are critical for determining regulations that optimize fishery outputs and conserve stocks. Each parameter was changed by 20% in the direction that would render the population more resilient to exploitation and then we evaluated how application of regulations chosen with this optimistic scenario would play out when in reality the stock is less productive and hence, less resilient to exploitation. Hence, we evaluated the impact of basing regulation choices on an M that is 20% higher, a CR that is 20% higher, an L_{mat} that is 20% lower and an F that is 20% lower than in reality.

Results

The two life histories revealed similar patterns in terms of yield, trophy catch and harvest numbers,

Table 2 Parameter input values and information sources used for simulations of Murray cod (*Maccullochella peelii*, Percichthyidae), lake trout (*Salvelinus namaycush*, Salmonidae), Eurasian perch (*Perca fluviatilis*, Percidae), arctic grayling (*Thymallus arcticus*, Salmonidae), zander (*Sander lucioperca*, Percidae) and northern pike (*Esox lucius*, Esocidae).

Parameter	Murray cod	Lake trout	Eurasian perch	Arctic grayling	Zander	Northern pike
R_0	1 000 000	1 000 000	1 000 000	1 000 000	1 000 000	1 000 000
A	40[3]	38[3]	10[3]	16[3]	16[9]	16[3]
M	0.11[1]	0.12[7]	0.44[4]	0.27[4]	0.27[9]	0.28[4]
CR	30[1]	24[11]	9.5[11]	24[11]	9.5[11]	6.1[11]
$\overline{L}_\infty$	1200[1]	872[7]	278[8]	370[5]	818[10]	976[9]
$L_{\infty,\min}$	960[2]	698[2]	222[2]	296[2]	654[2]	781[4]
$L_{\infty,\max}$	1440[2]	1046[2]	334[2]	444[2]	982[2]	1171[4]
k	0.11[1]	0.092[7]	0.29[8]	0.18[5]	0.24[10]	0.19[9]
t_o	0[1]	0[7]	0[8]	−1.75[5]	−0.01[10]	−0.34[9]
L_{mat}	500[1]	520[7]	151[8]	230[9]	456[9]	378[9]
α	3.6×10^{-5} [1]	5.9×10^{-5} [7]	5.9×10^{-4} [8]	1.9×10^{-4} [9]	4.7×10^{-5} [10]	5.8×10^{-5} [9]
β	2.91[1]	3.18[7]	3.18[8]	2.92[9]	3.16[10]	3.07[9]
L_{min}	500	520	151	230	456	378
L_{cap}	300[12]	218[12]	70[12]	93[12]	205[12]	244[12]
L_{troph}	1020[6]	741[6]	236[6]	315[6]	695[6]	830[4]

[1]Citations in Allen *et al.* (2009).
[2]$\overline{L}_\infty \pm 0.2 * \overline{L}_\infty$.
[3]Hoenig (1983).
[4]Jensen (1996).
[5]Hughes (1997).
[6]$0.85 * L_{\infty,\max}$.
[7]Shuter *et al.* (1998).
[8]Heibo *et al.* (2005).
[9]Fishbase (Froese and Pauly 2006).
[10]Wysujack *et al.* (2002).
[11]Myers *et al.* (1999).
[12]$0.25 * \overline{L}_\infty$.

and corresponding trade-offs, between regulation types (Figs 1 and 2). Liberal regulations (i.e. wide HSs or low MLLs) that produced high harvest provided low trophy catch for both regulation types and fishing mortality levels. Accordingly, restricting harvest by increasing the MLL or by decreasing the upper bound of the HS resulted in an increase in the catch of trophy fish, with maximum trophy catch being realized by a full harvest closure (i.e. total catch-and-release fishery; Figs 1 and 2). Biomass yield was found to reach a maximum for both fishing exploitation level in both life-history prototypes (Figs 1c,d and 2b-d), indicating that our high fishing mortality level resulted in growth and recruitment overfishing for liberal regulations. Catches of trophy fish were eliminated for liberal regulations unless fishing mortality was low (Figs 1b,d and 2b,d). In the LLLP prototype, no dome-shaped yield curve was predicted for HSs (Fig. 1a,b), while a MLL was present that maximized yield (Fig. 1c,d). In the SLHP life-history prototype, maximum yield was predicted at the high fishing mortality for a narrow HS and a small MLL (Fig. 2b,d). This life-history prototype also revealed a very pronounced dome-shaped relationship of regulations and maximum harvest numbers for the high exploitation rate, which was not the case in the less productive LLLP life-history prototype.

In terms of management objectives, regulations that favoured trophy catch over harvest were found to result in more restrictive regulations (e.g. higher MLLs or narrower HSs), while more liberal regulations were needed to meet harvest objectives (Table 3). Regulations that met compromise objectives were always intermediate, suggesting a trade-off among trophy catch and harvest (Table 3). The HS regulations generally provided higher values of all metrics except biomass yield compared with MLLs for all management objectives (compromise, trophy and harvest) and fishing mortality rates. Values of harvest, trophy catch,

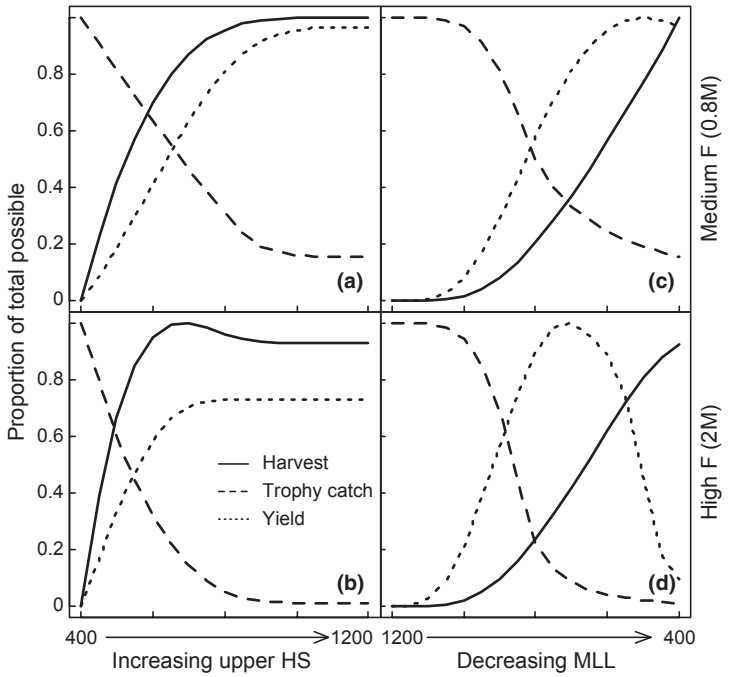


Figure 1 The proportion of the maximum possible harvest, trophy catch and biomass yield produced with a range harvest slots (left panels, a and b) and with a range of minimum-length limits (right panels, c and d) applied to a long-lived, low-productive fish population (LLLP) (Table 1). Panels a and c represent a fishery with medium exploitation (F = 0.8*M*, *M* = instantaneous annual natural mortality rate) and panels b and d represent a fishery with high exploitation (F = 2*M*). Left panels, a and b, describe a change in the upper limit of a harvest slot (HS) with a lower limit of 400 mm total length. Right panels, c and d, describe a change in the minimum-length limit (MLL).

SPR and *J* were nearly always higher with the best-performing HS regulations than for the best MLL (Table 3). This was true across life-history types, fishing mortality rates and management objectives, suggesting that improved performance of the HS regulations was a general result. The relative gains in harvest and trophy fish when applying the HS over the MLL were greater for the high exploitation fishery and for the LLLP prototype than for the medium exploitation and SLHP prototype. Biomass yield was the only metric that was nearly always higher for MLLs compared with HSs (Table 3).

High levels of fishing mortality resulted in more conservative regulations being required to meet each management objective. For example, the preferred HS narrowed and MLL increased as fishing mortality levels went from medium to high for both life-history types (Table 3). However, under conditions of high exploitation, the advantage of a HS over a MLL for meeting management objectives was particularly pronounced. For example, for the LLLP under low exploitation (0.8*M*) with a harvest-based management objective, the objective-meeting HS produced a harvest of 210 000 and trophy catch of 14 400 fish, while the objective-meeting MLL produced a harvest of 144 000 and trophy catch of 9 900 fish (Table 3). This represented a 46 and 45% increase in harvest and trophy catch, respectively, for the HS over the MLL. Under high exploitation (2*M*), the HS produced an 170 and 176% increase in harvest and trophy catch, respectively, indicating a strongly increased benefit of HSs over MLLs under high exploitation. This pattern was consistent across the two life-history strategies and the three management objectives (Table 3) and indicated that the greatest advantage of a HS over a MLL would be realized for fisheries with high exploitation rates. These general findings resulted because HSs restricted the harvest to smaller, more abundant ages (sizes) whereas the MLLs targeted larger, less abundant ages. As a result, HS regulations increased harvest while preserving old and large members of the stock to serve as trophy catch and a fecundity reserve to maintain recruitment.

Although the optimal HS for each management objective produced higher harvest and catch of

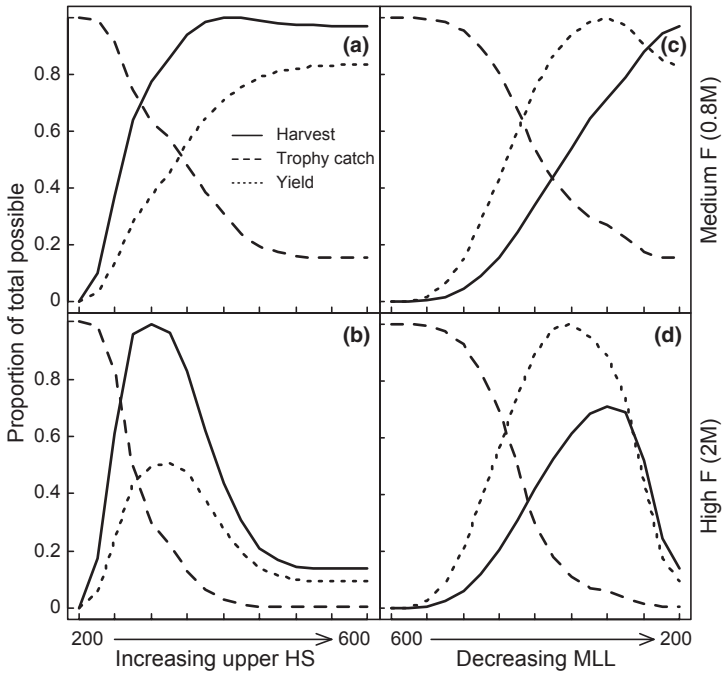


Figure 2 The proportion of the maximum possible harvest, trophy catch and biomass yield produced with a range harvest-slot limits (left panels, a and b) and with a range of minimum-length limits (right panels, c and d) applied to a short-lived, high-productive fish population (SLHP) (Table 1). Panels a and c represent a fishery with medium exploitation (F = 0.8*M*, *M* = instantaneous annual natural mortality rate) and panels b and d represent a fishery with high exploitation (F = 2*M*). Left panels, a and b, describe a change in the upper limit of a harvest slot (HS) with a lower limit of 200 mm total length. Right panels, c and d, describe a change in the minimum-length limit (MLL).

trophy fish than MLLs, this occurred at the expense of biomass yield. In fact, MLLs revealed a greater potential for yields than HSs across the full range of each regulation, particularly for the SLHP and the high exploitation fisheries (Figs 1 and 2). For example, the MLL meeting the compromise management objective produced approximately 112% greater yield than the corresponding HS for the LLLP and about 167% greater yield than the compromise HS for the SLHP at low exploitation (Table 3). The clear advantage of MLLs for producing higher biomass yields at each management objective was not noticeably influenced by the life-history strategy or the level of exploitation.

With few exceptions, both MLLs and HSs achieved conservation objectives in terms of SPR at each of the three objectives (Table 3). However, the use of the HSs resulted in a greater proportion of the total annual fecundity being produced by older fish (*J*) compared with MLLs (Table 3). This pattern was consistent across all management objectives, exploitation levels and life-history types. Thus, HSs placed on intermediate-age/size fish produced higher harvests and catches of trophy fish, while meeting conservation thresholds for SPR and for conserving the fecundity produced by older fish for nearly all scenarios simulated. The only case where this was not true was when the LLLP was managed for harvest with the optimal HS while being exploited at high rates. Under these conditions, the MLL outperformed the HS for maintaining high SPR values (Table 3). MLLs were effective at maximizing biomass yields and were similarly effective at conserving the spawning stock (SPR). Nevertheless, conservation performance was nearly always better with HS than MLL regulations.

We found the relative performance of HSs and MLLs was consistent across the five simulated fish species and mirrored the findings for the two prototypical life histories just described (Table 4). Increases in harvest, trophy catch and proportion of total annual fecundity resulting from older fish (*J*) were always realized by the application of the objective-meeting HS over the corresponding MLL for all five species (Table 4). By contrast, across all species MLLs resulted in greater biomass yield at each of the management objectives (Table 4).

Table 3 The performance of harvest slot (HS) and minimum-length limit (MLL) regulations for two different life-history prototypes, three management objectives and two fishing mortality levels *F*. The LLLP life history represents a long-lived, low-productive fish population, while the SLHP life history represents a short-lived, high-productive fish population (Table 1). Bold values indicate the best performance for each metric.

Life-history prototypes	Management objectives	*F*	Regulation (mm)	Harvest (thousands)	Trophy (thousands)	Yield (million kg)	SPR	*J*
LLLP	Compromise	0.8*M*	400–584 HS	**146**	**29.9**	0.17	**0.67**	**0.45**
		0.8*M*	712 MLL	77	15.6	**0.36**	0.69	0.28
	Compromise	2*M*	400–492 HS	**180**	**65.6**	0.16	**0.63**	**0.46**
		2*M*	802 MLL	67	23.9	**0.37**	0.71	0.27
	Trophy	0.8*M*	400–466 HS	**64**	**39.5**	0.05	**0.88**	**0.46**
		0.8*M*	816 MLL	40	24.4	**0.24**	0.62	0.36
	Trophy	2*M*	400–436 HS	**81**	**88.2**	0.06	**0.85**	**0.46**
		2*M*	854 MLL	44	48.1	**0.28**	0.80	0.34
	Harvest	0.8*M*	400–846 HS	**210**	**14.4**	0.40	0.40	**0.29**
		0.8*M*	504 MLL	144	9.9	**0.46**	**0.45**	0.22
	Harvest	2*M*	400–636 HS	**273**	**32.8**	0.35	0.29	**0.39**
		2*M*	716 MLL	101	11.9	**0.48**	**0.55**	0.15
SLHP	Compromise	0.8*M*	200–284 HS	**169**	**60.5**	0.03	**0.76**	**0.36**
		0.8*M*	376 MLL	105	37.7	**0.08**	0.75	0.21
	Compromise	2*M*	200–257 HS	**204**	**127.2**	0.03	**0.75**	**0.36**
		2*M*	411 MLL	103	63.7	**0.09**	0.73	0.17
	Trophy	0.8*M*	200–246 HS	**76**	**81.0**	0.01	**0.92**	**0.37**
		0.8*M*	429 MLL	56	60.2	**0.06**	0.86	0.28
	Trophy	2*M*	200–235 HS	**90**	**163.1**	0.01	**0.92**	**0.37**
		2*M*	446 MLL	61	113.0	**0.06**	0.84	0.26
	Harvest	0.8*M*	200–422 HS	**239**	**28.7**	0.07	0.52	**0.27**
		0.8*M*	265 MLL	180	21.7	**0.09**	**0.57**	0.15
	Harvest	2*M*	200–318 HS	**276**	**57.3**	0.05	0.48	**0.33**
		2*M*	366 MLL	146	29.8	**0.10**	**0.61**	0.10

M, instantaneous annual natural mortality rate, SPR, spawning potential ratio, *J*, proportion of fecundity produced by the older half of age classes in the population.

Additionally, SPR at the management objective was generally similar between the objective-meeting HS and MLL. Few exceptions occurred for high exploitation fisheries managed for harvest using HS, which reduced the SPR relative to MLL (Table 4). However, in all cases, the SPR was still above 0.35 (results not shown).

Discard mortality had little influence on the relative performance of HSs versus MLLs; however, it influenced the conservation objectives and the harvesting efficiency of the fishery. Moderate levels of discard mortality (10%) had minimal effects on the results, but high levels of discard mortality (30%) rendered both MLLs and HSs ineffective for maintaining SPR under conditions of high fishing mortality (Table 5). For example, both the LLLP and SLHP had SPR values ≤ 0.35 when discard mortality was 30% and exploitation was $2M$ (Table 5), with the exception of the SLHP managed for trophy catch. We found HSs to maintain harvesting efficiency (E) in the face of discard mortality, particularly when exploitation rates were high. Under high exploitation rates, the efficiency of the fishery could be doubled when applying the

Table 4 The percent change in the performance metrics when changing the regulation from the objective-meeting minimum-length limit to the objective-meeting harvest slot for a range of species (Table 2), three management objectives (compromise, trophy and harvest, Table 3) and two fishing mortality levels F.

Life history	Management objective	F	Harvest	Trophy	Yield	SPR	J
Murray cod	Compromise	0.8M	45	46	−38	6	40
		2M	76	76	−41	5	68
	Trophy	0.8M	22	25	−66	10	21
		2M	39	30	−64	13	32
	Harvest	0.8M	13	12	−10	0	23
		2M	80	80	−16	−21	109
Lake trout	Compromise	0.8M	51	52	−60	3	94
		2M	89	87	−69	1	181
	Trophy	0.8M	27	30	−83	9	48
		2M	38	40	−85	13	78
	Harvest	0.8M	17	17	−21	−2	61
		2M	90	90	−46	−26	402
Eurasian perch	Compromise	0.8M	46	43	−26	3	47
		2M	69	76	−28	3	86
	Trophy	0.8M	21	23	−57	9	26
		2M	38	30	−54	10	40
	Harvest	0.8M	11	12	−6	0	27
		2M	73	79	−3	−21	135
Arctic grayling	Compromise	0.8M	56	53	−43	0	31
		2M	88	86	−46	0	44
	Trophy	0.8M	25	32	−71	7	16
		2M	44	37	−69	8	20
	Harvest	0.8M	22	21	−13	−5	21
		2M	90	95	−24	−25	69
Zander	Compromise	0.8M	82	84	−69	2	66
		2M	133	134	−73	−2	81
	Trophy	0.8M	46	46	−86	6	30
		2M	49	48	−88	7	40
	Harvest	0.8M	52	51	−36	−13	75
		2M	138	140	−56	−28	167
Northern pike	Compromise	0.8M	40	38	−50	5	54
		2M	57	57	−57	8	98
	Trophy	0.8M	15	19	−75	8	28
		2M	21	21	−76	10	39
	Harvest	0.8M	12	13	−16	1	38
		2M	64	67	−33	−15	181

M, instantaneous annual natural mortality rate, SPR, spawning potential ratio, J, proportion of fecundity produced by the older half of age classes in the population.

objective-meeting HS over the corresponding MLL for both life-history strategies (Table 5). However, under conditions of high discard mortality, applying either a HS or MLL to meet recreational fisheries management objectives may not be an effective strategy for long-term conservation of the stock.

Results on the performance of HSs over MLLs were robust to parameter uncertainty indicating management with imperfect knowledge of key productivity parameters *M*, *CR*, *F* and L_{mat} would not alter the relative performance of HSs over MLLs (Appendix A, Tables S1–S4). In only one case did the relative performance of HSs and MLLs reverse. This reversal occurred for the trophy-oriented objective applied to the SLHP undergoing medium exploitation. In this case, the harvest numbers produced by the optimal MLL were greater than the HS; however, there were few differences among the policies (Appendix A, Tables S1–S4). The percent change of metrics in response to changing each of the parameters by 20% ranged from −92 to 55%, but in over 90% of the cases, metrics varied only between −20% and 20% indicating inelastic responses, low sensitivity and a comparatively robust model. These results inferred that HSs would outperform MLLs even with substantial uncertainty in population and fishery parameters.

Discussion

We showed that HSs produced a more favourable compromise among fishery and conservation objectives than MLLs for a range of management objectives that included harvest, compromise and trophy catches. This effect stemmed from HS regulations protecting large fecund as well as immature fish in the population from harvest, thereby

Table 5 The performance of harvest slots (HS) and minimum-length limits (MLL) regulations for two prototypical fish life histories under two levels of discard (hooking) mortality *D* with respect to three management objectives at two fishing mortality levels *F*. Long-lived, low productive (LLLP), short-lived, high productive prototype (SLHP) (Table 1).

			D = 10%			D = 30%		
Life-history prototype	Management objective	*F*	Regulation (mm)	SPR	*E*	Regulation (mm)	SPR	*E*
LLLP	Compromise	0.8*M*	400–588 HS	0.60	**0.83**	400–604 HS	**0.48**	**0.65**
		0.8*M*	698 MLL	**0.62**	0.64	646 MLL	**0.48**	0.43
	Compromise	2*M*	400–490 HS	0.46	**0.69**	400–496 HS	0.26	**0.46**
		2*M*	782 MLL	**0.53**	0.35	726 MLL	**0.30**	0.16
	Trophy	0.8*M*	400–468 HS	**0.76**	**0.60**	400–470 HS	**0.59**	**0.35**
		0.8*M*	800 MLL	0.73	0.45	766 MLL	0.56	0.23
	Trophy	2*M*	400–436 HS	**0.60**	**0.44**	400–436 HS	**0.33**	**0.22**
		2*M*	832 MLL	0.59	0.25	788 MLL	0.32	0.09
	Harvest	0.8*M*	400–794 HS	0.40	**0.92**	400–846 HS	0.35	**0.80**
		0.8*M*	540 MLL	**0.46**	0.83	464 MLL	**0.37**	0.72
	Harvest	2*M*	400–600 HS	0.27	**0.84**	400–628 HS	0.17	**0.66**
		2*M*	716 MLL	**0.44**	0.48	646 MLL	**0.24**	0.27
SLHP	Compromise	0.8*M*	200–271 HS	**0.67**	**0.77**	200–281 HS	**0.54**	**0.54**
		0.8*M*	372 MLL	**0.67**	0.64	345 MLL	0.53	0.40
	Compromise	2*M*	200–252 HS	**0.56**	**0.62**	200–249 HS	**0.34**	**0.29**
		2*M*	404 MLL	**0.56**	0.41	391 MLL	**0.34**	0.15
	Trophy	0.8*M*	200–248 HS	**0.80**	**0.52**	200–248 HS	**0.63**	**0.27**
		0.8*M*	422 MLL	0.77	0.44	407 MLL	0.60	0.21
	Trophy	2*M*	200–241 HS	**0.66**	**0.35**	200–239 HS	**0.37**	**0.12**
		2*M*	434 MLL	0.62	0.27	420 MLL	0.36	0.08
	Harvest	0.8*M*	200–391 HS	0.48	**0.90**	200–412 HS	0.41	**0.75**
		0.8*M*	272 MLL	**0.53**	0.82	254 MLL	**0.43**	0.67
	Harvest	2*M*	200–273 HS	0.39	**0.80**	200–267 HS	0.26	**0.52**
		2*M*	371 MLL	**0.49**	0.54	346 MLL	**0.30**	0.25

M, instantaneous annual natural mortality rate, SPR, spawning potential ratio, *E*, harvesting efficiency, which is the fraction of dead fish that are harvested rather than dying due to catch-and-release related hooking mortality.
Bold values indicate the regulation producing the best performance for each metric.

providing not only greater trophy catch and less size truncation, but also increasing the total number of fish harvested and improved harvesting efficiency in the context of discard mortality. These benefits of HS regulations came at a cost of biomass yields and smaller size of fish harvested (as indicated by the size of the legal length range of each regulation); however, the trade-off of biomass yield for numerical harvest when HSs are applied over MLLs is probably an attractive compromise for many recreational fisheries because it would allow more anglers to harvest fish than expected with a yield-maximizing MLL, while at the same time maintaining trophy fish catch and meeting conservation goals (Jensen 1981).

Harvest-based management objectives are often perceived to be in conflict with conservation-based objectives (Aplet *et al.* 1992; Hilborn 2007; Koehn 2010; Koehn and Todd 2012). While the shared goal of long-term sustainability can serve both conservation and human needs (but see Niesten and Rice 2004), sacrifices to exploitation goals over shorter time frames can be necessary to meet long-term conservation objectives (Secor 2000; Foley *et al.* 2005; Cheung and Sumaila 2008). Our model identified regulations where fisheries-based and conservation-based objectives are not necessarily in conflict when using appropriately narrow HSs targeting intermediate-sized mature fish. In fact, the implementation of HSs may provide necessary protection to stock age-structure and spawning stock size with little sacrifice to angler benefits, because angler satisfaction is positively related to harvest opportunities and size of fish captured for many angler types (Arlinghaus 2006). Thus, according to our model and others developed previously for specific fish species (e.g. Jensen 1981; Arlinghaus *et al.* 2010; García-Asorey *et al.* 2011; Koehn and Todd 2012), HS regulations are likely more effective at collectively meeting multiple fishery and conservation objectives than MLLs and could simultaneously improve angler satisfaction and achieve biological sustainability. Hence, HSs appear to constitute a very promising tool for many recreational fisheries because they outperform MLLs for all life histories analysed at both fishing effort levels and for all three management objectives. This statement obviously only applies when harvest numbers and number of trophy fish captured is more important to anglers than total yield or harvest of trophy fish.

We found that high discard mortality rates paired with high exploitation rates rendered both MLL and HS regulations ineffective in meeting conservation goals. These findings corroborate Coggins *et al.* (2007) who found that discard mortality could prevent sustainability of some fish stocks managed by length-based regulations. For these cases, other approaches are necessary to meet conservation goals such as temporal and/or spatial closures (Gwinn and Allen 2010) or even effort controls (Cox and Walters 2002). Alternatively, when discard mortality rates are low to moderate (e.g. <30%), the use of HSs to reduce exploitation, increase harvesting efficiency and conserve a more natural age-structure of stocks provides an option superior to MLLs that can potentially meet both long-term fishery and conservation objectives with less sacrifice to short-term fishery use. This is particularly important because fishery closures or effort controls can cause economic hardship to local communities built around recreational fisheries and will create other social costs such as stakeholder conflict (Cox and Walters 2002; Martinet *et al.* 2010).

For simplicity of presentation, we chose three management objectives that differentially weighted the social and economic value of harvest relative to trophy catch. These weightings are unlikely to represent universal objectives in recreational fisheries because angler communities vary in values and because weights attached to normative criteria will vary with managers and local culture (Fenichel *et al.* 2013). However, our model was general and we simulated the full range of size-based regulations for both MLLs and HSs. This allows the reader to choose any location on the *x*-axes of Figs 1 and 2 to trade-off among harvest, yield and trophy catch and thereby determine regulations that meet any objective along these three metrics. For example, the compromise management objective of the LLLP and high exploitation fishery was met with a narrow HS of 400–492 mm; however, the management objective of a fishery that values harvest exclusively would be met by setting the HS to 400–680 mm (Fig. 1b). Thus, our results can provide both general guidance for the application of length-based regulations and specific guidance when the weighting of specific (catch or harvest-dependent) normative criteria is known for a specific fishery.

Although protecting large and old fish with HSs is not a common fisheries regulation in practice,

some previous studies have implicated the advantages of HSs over alternative regulations for managing fisheries. Froese (2004), for example, presented four indices of overfishing and recommended the use of narrow harvest windows on recently mature fish (similar to the compromise HS regulations in this study) to prevent overfishing of commercial stocks. Berkeley *et al.* (2004a) suggested that implementation of HSs when discard mortality was low could preserve natural age composition and promote sustainability of groundfish stocks. Jensen (1981) reported that HSs increase trophy trout in the catch without strongly reducing yield, and Francis *et al.* (2007) suggested that protecting old fish is required for ecosystem-based fisheries management mentioning HSs as one of three management options for achieving objectives. Additionally, HSs have been highlighted for managing recreational fisheries targeting populations that experience a range of size-dependent maternal effects on egg and larval quality (Arlinghaus *et al.* 2010; Venturelli *et al.* 2010). However, benefits of HSs over MLLs in terms of harvest numbers and catch of trophies are not contingent on maternal effects (Arlinghaus *et al.* 2010). In fact, size-dependent maternal effects on offspring quality would enhance the benefits of HSs as reported in this article. Harvest-slot regulations are currently in place for some popular freshwater (e.g. white sturgeon, *Acipenser transmontanus,* Acipenseridae) and saltwater recreational fisheries in the USA. (e.g. red drum *Sciaenops ocellatus*, Sciaenidae and common snook *Centropomus undecimalis*, Centropomidae in Florida), but are overall far less common than MLL regulations. This work represents the first synthesis of the potential benefits of HSs to meet multiple fisheries and conservation objectives for recreational fisheries exploiting stocks across a range of life histories and therefore has general implication for a wide range of recreational fisheries that value both harvest numbers and trophy catch.

Like most modelling efforts, our results are contingent on model structure and other assumptions. For example, we assumed that compliance to regulations by anglers was 100%, which may not be realistic in some cases (Pierce and Tomcko 1998; Sullivan 2002). Non-compliance at levels reported elsewhere (e.g. 29% in northern pike fishing in Minnesota, Pierce and Tomcko 1998) would likely reduce the ability of both HSs and MLLs to meet fishery objectives and conserve stocks. Additionally, reproductive senescence has been reported in some species (Reznick *et al.* 2004). Our predictions might overestimate the effects of HS limits for these species that demonstrate a loss of fecundity or egg/larval quality at very old ages. Such effects are however unlikely to be very prevalent in most exploited stocks because few fish reach maximum age under fished conditions, and reproductive senescence may not be universally present across species (e.g. Kishi *et al.* 2003). As a further limitation, we did not model density-dependent growth or survival in the post-recruited ages. How this impacts our results will depend on the range of size/age of fish that the density dependence occurs and the strength of density dependence. Lorenzen (2005) argued that density-dependent survival in the recruited stage is unlikely to be a relevant process in many fish stocks, but density-dependent growth is probably common and affect all life stages to some degree (Lorenzen and Enberg 2002). It is a safe assumption that the presence of density-dependent growth should render the stock more resilient to fishing and will thus likely widen HSs and reduce yield-maximizing MLLs (Beverton and Holt 1957). Without detailed knowledge on the density dependence in specific life stages, it is impossible to predict the relative performance of HSs and MLLs; however, HSs provide the flexibility to create ecologically sensitive regulations that target populations at the life-stage of greatest density dependence or over production. The only available study that has considered density-dependent growth comparing HSs and MLLs has been conducted in northern pike (Arlinghaus *et al.* 2010), whose results agree with the findings reported here. Future research should evaluate the performance of regulations in the presence of density-dependent growth and size-dependent survival across a range of life histories (Lorenzen 2005). Explicitly representing food-dependent growth and size-dependent predation in size-structured models may alter predictions on regulatory performance relative to more standard age-structured models (Van Kooten *et al.* 2007; Persson and de Roos 2013) like the model employed here.

In general, we believe that our predicted advantages of HSs over MLLs may be conservative for some fish species because we did not model factors, such as size-dependent maternal effects on the recruitment process, non-linear population dynamics rates or fishery-induced evolution, all of which can be affected by size-selective exploita-

tion. For example, Venturelli *et al.* (2010) provided evidence for age-dependent maternal effects on recruitment in walleye (*Sander vitreum*, Percidae) showing that the maximum reproductive rate in Lake Erie increased by 2.75-fold as the mean age of the stock shifted from 3.03 to 4.44 years. Furthermore, they demonstrated with a simulation study that the maximum reproductive rate of walleye could be increased by 1.2-fold by managing exploitation with a HS on age 2–4 fish vs. harvest strategies that targeted older ages (e.g. MLL, see also Arlinghaus *et al.* 2010). Our simulations did not account for size-dependent maternal effects on offspring performance as demonstrated previously for a range of species (e.g. Berkeley *et al.* 2004b; Venturelli *et al.* 2009; Arlinghaus *et al.* 2010) and therefore likely produced predictions of harvest and catch lower than would be expected for HSs applied to stocks that demonstrate size-dependent maternal effects (Arlinghaus *et al.* 2010).

Because we investigated long-term equilibrium states, we also did not account for the influence of environmental or demographic stochasticity amplifying non-linear population dynamical processes on the performance of the length-based regulations evaluated. Anderson *et al.* (2008) investigated mechanisms for destabilization of fish stocks due to exploitation. The authors concluded that the mechanism with the most support was that age truncation due to size-selective exploitation causes increased fluctuations in fish abundance (see also Hidalgo *et al.* 2011; Rouyer *et al.* 2011). Hsieh *et al.* (2010) showed that this effect held across species (but see Lobón-Cervia 2011 for an alternative view for exploited brown trout, *Salmo trutta*, Salmonidae). Therefore, the current body of evidence suggests that fishery-induced age truncation can lead to higher probability of fishery crashes and local extinctions (Lande *et al.* 2003), and our results suggest that HSs may represent a regulatory option that protects age composition which may reduce the likelihood of such catastrophic outcomes.

Finally, we omitted the potential for joint evolution of life-history traits such as age- and size-at-maturation, reproductive investments and juvenile growth rate, which all affect body size at adult age and may evolve in response to size-selective recreational fisheries (Matsumura *et al.* 2011). Law (2007) suggested the conservation of large fish to reduce the effects of fisheries-induced evolution. Supporting this view, Matsumura *et al.* (2011) found that MLLs exerted the most negative impact on body size evolution due to negative selection on growth rate and size at maturation. Although intermediate HSs would not eliminate the selection pressures on all life-history traits, such regulations would lead to selection on large juvenile growth, which may increase (rather than decrease) adult fish size and yield in the long term. Therefore, the conclusion that HSs are superior to MLLs would also hold if fisheries-induced evolution would be present.

Our results suggested a greater potential for improvement in fishery performance with HSs than MLLs across a range of management objectives, life histories and fishing mortality rates. Therefore, we suggest that a new perspective on managing recreational fisheries using length-based management tools is needed in situations where both harvest numbers and trophy catch matter to stakeholders. Under these conditions, rather than relying on retention of large fish to maximize biomass yields, we contend that HS regulations will provide the most favourable compromise among multiple fisheries and conservation objectives. Because our results were robust to life history, management objective and the fishing mortality rates, HS regulations should be considered preferable over MLLs for many recreational fisheries that value harvest and size of fish in the catch. Depending on the local customs and culture, a manager can choose to meet either harvest numbers or trophy catch objectives by varying the width of the HS. We recommend empirical studies that test some of the predictions of the present model because the results promise far-reaching implications for recreational-fisheries management that is currently mainly based on MLLs.

Acknowledgements

Funding was received by R.A. through the project Besatzfisch (www.besatz-fisch.de, grant # 01UU 0907) granted by the German Federal Ministry for Education and Research (BMBF) in the Program on Social-Ecological Research. R.A. gratefully acknowledges the University of Florida, School of Forest Resources and Conservation for sabbatical support during which a portion of the present article was drafted. We thank two reviewers for helpful comments on an earlier version of this article.

References

Allen, K.R. (1953) A method for computing the optimum size-limit for a fishery. *Nature* **172**, 210–210.

Allen, M.S. and Pine, W.E. III (2000) Detecting fish population responses to a minimum length limit: effects of variable recruitment and duration of evaluation. *North American Journal of Fisheries Management* **20**, 672–682.

Allen, M.S., Myers, R.M. and Walters, C.J. (2008) Temporal trends in largemouth bass mortality, with fisheries implications. *North American Journal of Fisheries Management* **26**, 108–118.

Allen, M.S., Brown, P., Douglas, J., Fulton, W. and Catalano, M. (2009) An assessment of recreational fishery harvest policies for Murray cod in southeast Australia. *Fisheries Research* **95**, 260–267.

Allen, M., Hanson, M.J., Ahrends, R. and Arlinghaus, R. (2013) Dynamic angling effort influences the value of minimum-length limits to prevent recruitment overfishing. *Fisheries Management and Ecology* **20**, 247–257.

Anderson, L.G. (1993) Toward a complete economic theory of the utilization and management of recreational fisheries. *Journal of Environmental Economics and Management* **24**, 272–295.

Anderson, C.N.K., Hsieh, C., Sandin, S.A. *et al.* (2008) Why fishing magnifies fluctuations in fish abundance. *Nature* **452**, 835–839.

Aplet, G.H., Laven, R.D. and Fiedler, P.L. (1992) The relevance of conservation biology to natural resource management. *Conservation Biology* **6**, 298–300.

Arlinghaus, R. (2006) On the apparently striking disconnect between motivation and satisfaction in recreational fishing: the case of catch orientation of German anglers. *North American Journal of Fisheries Management* **26**, 592–605.

Arlinghaus, R., Mehner, T. and Cowx, I.G. (2002a) Reconciling traditional inland fisheries management and sustainability in industrialized countries, with emphasis on Europe. *Fish and Fisheries* **3**, 261–316.

Arlinghaus, R., Pfeifer, M., Grosch, U.A. and Wolter, C. (2002b) Fisheries in the river Spree catchment in former times and today. In: *Die Spree - Zustand, Probleme und Entwicklungsmoglichkeiten* (eds J. Köhler, J. Gelbrecht and M. Pusch). E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, pp. 210–220.

Arlinghaus, R., Cooke, S.J., Lyman, J. *et al.* (2007) Understanding the complexity of catch-and-release in recreational fishing: an integrative synthesis of global knowledge from historical, ethical, social, and biological perspectives. *Reviews in Fisheries Science* **15**, 75–167.

Arlinghaus, R., Matsumura, S. and Dieckmann, U. (2010) The conservation and fishery benefits of protecting large pike (*Esox lucius* L.) by harvest regulations in recreational fishing. *Biological Conservation* **143**, 1444–1459.

Bartholomew, A. and Bohnsack, J.A. (2005) A review of catch-and-release angling mortality with implications for no-take reserves. *Reviews in Fish Biology and Fisheries* **15**, 129–154.

Beamish, R.J., McFarlane, G.A. and Benson, A. (2006) Longevity overfishing. *Progress in Oceanography* **68**, 289–302.

Berkeley, S.A., Hixon, M.A., Larson, R.J. and Love, M.S. (2004a) Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries* **29**, 23–32.

Berkeley, S.A., Chapman, C. and Sogard, S.M. (2004b) Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. *Ecology* **85**, 1258–1264.

von Bertalanffy, L. (1938) A quantitative theory of organic growth. *Human Biology* **10**, 181–213.

Beverton, R. and Holt, S. (1957) *On the Dynamics of Exploited Fish Populations*. Chapman and Hall, London.

Birkeland, C. and Dayton, P.K. (2005) The importance in fishery management of leaving the big ones. *Trends in Ecology and Evolution* **20**, 356–358.

Botsford, L. (1981a) Optimal fishery policy for size-specific, density-dependent population models. *Journal of Mathematical Biology* **12**, 265–293.

Botsford, L. (1981b) The effects of increased individual growth rates on depressed population size. *The American Naturalist* **117**, 38–63.

Botsford, L.W. and Hobbs, R.C. (1986) Static optimization of yield per recruit with reproduction and fishing costs. *Fisheries Research* **4**, 181–189.

Brousseau, C.S. and Armstrong, E.R. (1987) The role of size limits in walleye management. *Fisheries* **12**, 2–5.

Bryan, H. (1977) Leisure value systems and recreation specialization: the case of trout fishermen. *Journal of Leisure Research* **9**, 174–187.

Caddy, J.F. (1999) Fisheries management in the twenty-first century: will new paradigms apply? *Reviews in Fish Biology and Fisheries* **9**, 1–43.

Cheung, W.W.L. and Sumaila, U.R. (2008) Trade-offs between conservation and socio-economic objectives in managing a tropical marine ecosystem. *Ecological Economics* **66**, 193–210.

Clark, R.D. Jr, Alexander, G.R. and Growing, H. (1980) Mathematical description of trout-stream fisheries. *Transactions of the American Fisheries Society* **109**, 587–602.

Coggins, L.G., Catalano, M.J., Allen, M.S., Pine, W.E. and Walters, C.J. (2007) Effects of cryptic mortality and the hidden costs of using length limits in fishery management. *Fish and Fisheries* **8**, 196–210.

Coleman, F.C., Figueira, W.F., Ueland, J.S. and Crowder, L.B. (2004) The impact of United States recreational fisheries on marine fish populations. *Science* **305**, 1958–1960.

Conover, D.O. and Munch, S.B. (2002) Sustaining fisheries yields over evolutionary time scales. *Science* **297**, 94–96.

Cox, S.P. and Walters, C. (2002) Modeling exploitation in recreational fisheries and implications for effort management on British Columbia rainbow trout lakes. *North American Journal of Fisheries Management* **22**, 21–34.

Cox, S.P., Walters, C.J. and Post, J.R. (2003) A model-based evaluation of active management of recreational fishing effort. *North American Journal of Fisheries Management* **23**, 1294–1302.

Crutchfield, J.A. (1962) Valuation of fishery resources. *Land Economics* **38**, 145–154.

Daedlow, K., Beard, T.D. and Arlinghaus, R. (2011) A property rights-based view on management of inland recreational fisheries: contrasting common and public fishing right regimes in Germany and the United States. *American Fisheries Society Symposium* **75**, 13–38.

Dorow, M., Beardmore, B., Haider, W. and Arlinghaus, R. (2010) Winners and losers of conservation policies for European eel (*Anguilla anguilla* L.): an economic welfare analysis for differently specialised anglers. *Fisheries Management and Ecology* **17**, 106–125.

Dotson, J.R., Allen, M.S., Kerns, J.A. and Pouder, W.F. (2013) Utility of restrictive harvest regulations for trophy largemouth bass management. *North American Journal of Fisheries Management* **33**, 499–507.

Driver, B.L. (1985) Specifying what is produced by management of wildlife by public agencies. *Leisure Sciences* **7**, 281–295.

Dunning, D.J., Ross, Q. and Gladden, J. (1982) Evaluation of minimum size limits for St. Lawrence River northern pike. *North American Journal of Fisheries Management* **2**, 171–175.

Edeline, E., Carlson, S.M., Stige, L.C. *et al.* (2007) Trait changes in a harvested population are driven by dynamic tug-of-war between natural and harvest selection. *Proceedings of the National Academy of Science of the United States of America* **104**, 15799–15804.

Food and Agricultural Organization of the United Nations (FAO) (2012) *Technical Guidelines for Responsible Fisheries: Recreational Fisheries*. FAO, Rome, pp. 192.

Fenichel, E., Gentner, B. and Arlinghaus, R. (2013) Normative considerations for recreational fishery management: a bioeconomic framework for linking positive science and normative fisheries policy decisions. *Fisheries Management and Ecology* **20**, 223–233.

Fisher, M.R. (1997) Segmentation of the angler population by catch preference, participation, and experience: management-oriented application to recreation specialization. *North American Journal of Fisheries Management* **17**, 1–10.

Foley, J.A., DeFries, R., Asner, G.P. *et al.* (2005) Global consequences of land use. *Science* **309**, 570–574.

Francis, R.C., Hixon, M.A., Clarke, M.E., Murawski, S.A. and Ralston, S. (2007) Ten commandments for ecosystem-based fisheries scientists. *Fisheries* **32**, 217–233.

Freudenberg, P. and Arlinghaus, R. (2010) Benefits and constraints of outdoor recreation for people with physical disabilities: inferences from recreational fishing. *Leisure Sciences* **32**, 55–71.

Froese, R. (2004) Keep it simple: three indicators to deal with overfishing. *Fish and Fisheries* **5**, 86–91.

Froese, R. and PaulyD. (eds) (2006) *FishBase*. World Wide Web electronic publication. Available at: http://www.fishbase.org, version (3/2012) (accessed 1 December 2011).

García-Asorey, M.I., Escati-Penaloza, G., Parma, A.M. and Pascual, M.A. (2011) Conflicting objectives in trophy trout recreational fisheries: evaluating trade-offs using an individual-based model. *Canadian Journal of Fisheries and Aquatic Sciences* **68**, 1892–1904.

Goodwin, N.B., Grant, A., Perry, A.L., Dulvy, N.K. and Reynolds, J.D. (2006) Life history correlates of density dependent recruitment in marine fishes. *Canadian Journal of Fisheries and Aquatic Sciences* **63**, 494–509.

Goodyear, C.P. (1980) Compensation in fish populations. In: *Biological Monitoring of Fish* (eds C.H. Hocutt and J.R. Stauffer). D. C. Heath, Lexington, MA, pp. 253–280.

Grey, D.R. and Law, R. (1987) Reproductive values and maximum yield. *Functional Ecology* **1**, 327–330.

Gwinn, D.C. and Allen, M.S. (2010) Exploring population-level effects of fisheries closures during spawning: an example using largemouth bass. *Transactions of the American Fisheries Society* **139**, 626–634.

Heibo, E., Magnhagen, C. and Vollestad, L.A. (2005) Latitudinal variation in live-history traits in Eurasian perch. *Ecology* **86**, 3377–3386.

Hendee, J.C. (1974) A multiple-satisfaction approach to game management. *Wildlife Society Bulletin* **2**, 104–113.

Hidalgo, M., Rouyer, T., Molinero, J.C. *et al.* (2011) Synergistic effects of fishing-induced demographic changes and climate variation on fish population dynamics. *Marine Ecology Progress Series* **426**, 1–12.

Hilborn, R. (2007) Defining success in fisheries and conflicts in objectives. *Marine Policy* **31**, 153–158.

Hoenig, J.M. (1983) Empirical use of longevity data to estimate mortality rates. *Fishery Bulletin* **82**, 898–903.

Hsieh, C., Yamauchi, A., Nakazawa, T. and Wang, W.F. (2010) Fishing effects on age and spatial structures undermine population stability in fishes. *Aquatic Sciences* **72**, 165–178.

Hudgins, M.D. and Malvestuto, S.P. (1996) Minimum sociocultural and economic data requirements for optimum yield management of reservoir fisheries. In: *Multidimensional Approaches to Reservoir Fisheries Management* (eds L.E. Miranda and D.R. de Vries). American Fisheries Society, Bethesda, Maryland, pp. 223–235.

Hughes, N.F. (1997) Population processes responsible for larger-fish-upstream distribution patterns of Arctic grayling (*Thymallus arcticus*) in interior Alaskan runoff rivers. *Canadian Journal of Fisheries and Aquatic Sciences* **56**, 2292–2299.

Hühn, D. and Arlinghaus, R. (2011) Determinants of hooking mortality in freshwater recreational fisheries:

a quantitative meta-analysis. *American Fisheries Society Symposium* **75**, 141–170.

Hunt, L.M. (2005) Choice models and recreational fishing site choice: insights and future opportunities. *Human Dimensions of Wildlife* **10**, 153–172.

Ihde, J.F., Wilberg, M.J., Loewensteiner, D.A., Secor, D.H. and Miller, T.J. (2011) The increasing importance of marine recreational fishing in the US: challenges for management. *Fisheries Research* **108**, 268–276.

Jacobson, P.C. (1996) Trophy and consumptive value-per-recruit analysis for a walleye fishery. *North American Journal of Fisheries Management* **17**, 75–80.

Jensen, A.L. (1981) Optimum size limits for trout fisheries. *Canadian Journal of Fisheries and Aquatic Sciences* **38**, 657–661.

Jensen, A.L. (1996) Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. *Canadian Journal of Fisheries and Aquatic Sciences* **53**, 820–822.

Johnston, F.D., Arlinghaus, R. and Dieckmann, U. (2010) Diversity and complexity of angler behaviour drive socially optimal input and output regulations in a bioeconomic recreational-fisheries model. *Canadian Journal of Fisheries and Aquatic Sciences* **67**, 1507–1531.

Kishi, S., Uchiyama, J., Baughman, A.M., Goto, T., Lin, M.C. and Tsai, S.B. (2003) The zebrafish as a vertebrate model of functional aging and very gradual senescence. *Experimental Gerontology* **38**, 777–786.

Koehn, J.D. (2010) Conservation and utilisation: harnessing forces for better outcomes for native fishes. *Ecological Management and Restoration* **11**, 86–87.

Koehn, J.D. and Todd, C.R. (2012) Balancing conservation and recreational fishery objectives for a threatened fish species, the Murray cod, *Maccullochella peelii*. *Fisheries Management and Ecology* **19**, 410–425.

Lande, R., Engen, S. and Saether, B. (2003) *Stochastic Population Dynamics in Ecology and Conservation*. Oxford University Press, New York, NY.

Law, R. (2007) Fisheries-induced evolution: present status and future directions. *Marine Ecology Progress Series* **335**, 271–277.

Law, R., Plank, M.J. and Kolding, J. (2012) On balanced exploitation of marine ecosystems: results from dynamic size spectra. *ICES Journal of Marine Science* **69**, 602–614.

Lester, N.P., Shuter, B.J. and Abrams, P.A. (2004) Interpreting the von Bertalanffy model of somatic growth in fishes: the cost of reproduction. *Proceedings of the Royal Society of London Series B – Biological Sciences* **271**, 1625–1631.

Lewin, W.C., Arlinghaus, R. and Mehner, T. (2006) Documented and potential biological impacts of recreational fishing: insights for management and conservation. *Reviews in Fisheries Science* **14**, 305–367.

Lloret, J. and Font, T. (2013) A comparative analysis between recreational and artisanal fisheries in a Mediterranean coastal area. *Fisheries Management and Ecology* **20**, 148–160.

Lobón-Cervia, J. (2011) Why fishing does not magnify temporal fluctuations in the population abundance of stream-living salmonids. *Reviews in Fisheries Science* **19**, 249–256.

Lorenzen, K. (2005) Population dynamics and potential of fisheries stock enhancement: practical theory for assessment and policy analysis. *Philosophical Transactions of the Royal Society of London, Series B* **260**, 171–189.

Lorenzen, K. and Enberg, K. (2002) Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. *Proceedings of the Royal Society of London Series B – Biological Sciences* **269**, 49–54.

Mace, P.M. (1994) Relationships between common biological reference points used as thresholds and targets of fisheries management strategies. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 110–122.

Maceina, M.J., Bettoli, P.W., Finely, S.D. and DiCenzo, V.J. (1998) Analyses of the sauger fishery with simulated effects of a minimum size limit in the Tennessee River of Alabama. *North American Journal of Fisheries Management* **18**, 66–75.

Marshall, D., Heppell, S., Munch, S. and Warner, R. (2010) The relationship between maternal phenotype and offspring quality: do older mothers really produce the best offspring? *Ecology* **91**, 2862–2873.

Martinet, V., Thebaud, O. and Rapaport, A. (2010) Hare or tortoise? Trade-offs in recovering sustainable bioeconomic systems. *Environmental Modeling and Assessment* **15**, 503–517.

Matsumura, S., Arlinghaus, R. and Dieckmann, U. (2011) Assessing evolutionary consequences of size-selective recreational fishing on multiple life-history traits, with an application to northern pike (*Esox lucius*). *Evolutionary Ecology* **25**, 711–735.

Myers, R.A. and Mertz, G. (1998) The limits of exploitation: a precautionary approach. *Ecological Applications* **8**, 165–169.

Myers, R.A., Bowen, K.G. and Barrowman, N.J. (1999) Maximum reproductive rate of fish at low population sizes. *Canadian Journal of Fisheries and Aquatic Sciences* **56**, 2404–2419.

Myers, R., Taylor, J., Allen, M. and Bonvechio, T.F. (2008) Temporal trends in voluntary release of largemouth bass. *North American Journal of Fisheries Management* **28**, 428–433.

Nielsen, L.A. (1999) History of inland fisheries management in North America. In: *Inland Fisheries Management in North America*, 2nd edn (eds C.C. Kohler and W.A. Hubert). American Fisheries Society, Bethesda, MD, pp. 3–30.

Niesten, E. and Rice, R. (2004) Sustainable forest management and conservation incentive agreements. *International Forestry Review* **6**, 56–60.

Noble, R.L. and Jones, T.W. (1999) Managing fisheries with regulations. In: *Inland Fisheries Management in North America*, 2nd edn (eds C.C. Kohler and W.A. Hubert). American Fisheries Society, Bethesda, MD, pp. 455–480.

Novinger, G.D. (1984) Observations on the use of size limits for black basses in reservoirs. *Fisheries* **9**, 2–6.

O'Farrell, M.R. and Botsford, L.W. (2006) The fisheries management implications of maternal-age-dependent larval survival. *Canadian Journal of Fisheries and Aquatic Sciences* **63**, 2249–2258.

Ottersen, G., Stige, L.C., Durant, J.M. *et al.* (2013) Temporal shifts in recruitment dynamics of North Atlantic fish stocks: effects of spawning stock and temperature. *Marine Ecology Progress Series* **480**, 205–225.

Paukert, C.P., Klammer, J.A., Pierce, R.B. and Simonson, T.D. (2001) An overview of northern pike regulations in North America. *Fisheries* **26**, 6–13.

Pawson, M.G., Glenn, H. and Padda, G. (2008) The definition of marine recreational fishing in Europe. *Marine Policy* **32**, 339–350.

Persson, L. and de Roos, A.M. (2013) Symmetry breaking in ecological systems through different energetic efficiencies of juveniles and adults. *Ecology* http://dx.doi.org/10.1890/12-1883.1.

Pierce, R.B. (2010) Long term evaluations of length limit regulations for northern pike in Minnesota. *North American Journal of Fisheries Management* **30**, 412–432.

Pierce, R.B. and Tomcko, C.M. (1998) Angler noncompliance with slot length limits for northern pike in five small Minnesota lakes. *North American Journal of Fisheries Management* **18**, 720–724.

Pierce, R.B., Tomcko, C.M. and Schupp, D.H. (1995) Exploitation of northern pike in seven small North-Central Minnesota lakes. *North American Journal of Fisheries Management* **15**, 601–609.

Post, J.R., Sullivan, M., Cox, S. *et al.* (2002) Canada's recreational fishery: The invisible collapse? *Fisheries* **27**, 6–17.

Powers, J.E., Lackey, R.T. and Zuboy, J.R. (1975) Decision-making in recreational fisheries management: an analysis. *Transactions of the American Fisheries Society* **104**, 630–634.

Radomski, R.J., Grant, G.C., Jacobson, P.C. and Cook, M.R. (2001) Visions for recreational fishing regulations. *Fisheries* **26**, 7–18.

Redmond, L.C. (1986) The history and development of warmwater fish harvest regulations. In: *Reservoir Fisheries Management: Strategies for the 80s* (eds G.E. Hall and M.J. Van Den Avyle). American Fisheries Society, Bethesda, ML, pp. 186–195.

Reed, W.T. (1980) Age-specific harvesting in a nonlinear population model. *Biometrics* **36**, 579–593.

Reed, W.J. (1983) Recruitment variability and age structure in harvested animal populations. *Mathematical Biosciences* **65**, 239–268.

Reznick, D.N., Bryant, M.J., Roff, D., Ghalambor, C.K. and Ghalambor, D.E. (2004) Effect of extrinsic mortality on the evolution of senescence in guppies. *Nature* **431**, 1095–1099.

Ricker, W.E. (1945) A method for estimating minimum size limits for obtaining maximum yield. *Copeia* **1945**, 84–94.

Roedel, P.M. (1975) *Optimum Sustainable Yield as a Concept in Fisheries Management, (American Fisheries Society Special Publication 9)*. American Fisheries Society, Washington D.C., pp. 89.

Rouyer, T., Ottersen, G., Durant, J.M. *et al.* (2011) Shifting dynamic forces in fish stock fluctuations triggered by age truncation? *Global Change Biology* **17**, 3046–3057.

Saila, S.B. (1956) Estimates of the minimum size-limit for maximum yield and production of chain pickerel, *Esox niger* Le Sueur, in Rhode Island. *Limnology and Oceanography* **1**, 195–201.

Secor, D.H. (2000) Spawning in the nick of time? Effect of adult demographics on spawning behavior and recruitment in Chesapeake Bay striped bass. *ICES Journal of Marine Science* **57**, 403–411.

Shuter, B.J., Jones, M.L., Korver, R.M. and Lester, N.P. (1998) A general, life history based model for regional management of fish stocks: the inland lake trout (*Salvelinus namaycush*) fisheries of Ontario. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 2161–2177.

Sullivan, M.G. (2002) Illegal angling harvest of walleyes protected by length limits in Alberta. *North American Journal of Fisheries Management* **22**, 1053–1063.

Tesch, F.W. and Wehrmann, L. (1982) *Die Pflege der Fischbestände und –gewässer*. Parey Buchverlag, Berlin.

Van Kooten, T., Persson, L. and de Roos, A.M. (2007) Size-dependent mortality induces life-history changes mediated through population dynamical feedbacks. *The American Naturalist* **170**, 258–270.

Van Poorten, B.T., Cox, S.P. and Cooper, A.B. (2013) Efficacy of harvest and minimum size limit regulations for controlling short-term harvest in recreational fisheries. *Fisheries Management and Ecology* **20**, 258–267.

Venturelli, P.A., Shuter, B.J. and Murphy, C.A. (2009) Evidence for harvest-induced maternal influences on the reproductive rates of fish populations. *Proceedings of the Royal Society of London Series B – Biological Sciences* **276**, 919–924.

Venturelli, P.A., Murphy, C.A., Shuter, B.J. *et al.* (2010) Maternal influences on population dynamics: evidence from an exploited freshwater fish. *Ecology* **91**, 2003–2012.

Walters, C.J. and Martell, S.J.D. (2004) *Fisheries Ecology and Management*. Princeton University Press, Princeton, New Jersey.

Walters, C.J., Hilborn, R. and Christensen, V. (2008) Surplus production dynamics in declining and recovering fish populations. *Canadian Journal of Fisheries and Aquatic Sciences* **65**, 2536–2551.

Welcomme, R.L. (2001) *Inland Fisheries: Ecology and Management*. Fishing News Books, Blackwell Science, Oxford, pp. 358.

Wilde, G.R. (1997) Largemouth bass fishery responses to length limits. *Fisheries* **22**, 14–23.

Wootton, R.J. (1998) *Ecology of Teleost Fishes*, 2nd edn. Chapman and Hall, London, UK.

Wright, P.J. and Trippel, E.A. (2009) Fishery-induced demographic changes in the timing of spawning: consequence for reproductive success. *Fish and Fisheries* **10**, 283–304.

Wysujack, K., Kasprzak, P., Laude, U. and Mehner, T. (2002) Management of pikeperch stock in a long-term biomanipulated stratified lake: efficient predation vs. low recruitment. *Hydrobiologia* **479**, 169–180.

Xu, C., Schneider, D.C. and Rideout, C. (2013) When reproductive value exceeds economic value: an example from the Newfoundland cod fishery. *Fish and Fisheries* **14**, 225–233.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Sensitivity test of the performance of harvest slot (HS) and minimum-length limit (MLL) regulations with incorrect estimates of the instantaneous natural mortality (M) for two different life-history prototypes (Table 1).

Table S2. Sensitivity test of the performance of harvest slot (HS) and minimum-length limit (MLL) regulations with incorrect estimates of the recruitment compensation ratio (CR) for two different life-history prototypes (Table 1).

Table S3. Sensitivity test of the performance of harvest slot (HS) and minimum-length limit (MLL) regulations with incorrect estimates of the instantaneous fisheries exploitation rate (F) for two different life-history prototypes (Table 1).

Table S4. Sensitivity test of the performance of harvest slot (HS) and minimum-length limit (MLL) regulations with incorrect estimates of the length at maturations (L_{mat}) for two different life-history prototypes (Table 1).

SUPPORTING INFORMATION

Table S1. Sensitivity test of the performance of harvest slot (HS) and minimum-length limit (MLL) regulations determined with incorrect estimates of the instantaneous natural mortality (*M*) for two different life-history prototypes (Table 1). The LLLP represents a long-lived low-productive fish population, while the SLHP represents a short-lived high-productive fish population.To determine the best regulation *M* was increased to 20% greater than its default value (Table 1) and the regulation best meeting each of three management objectives at two fishing mortality levels *F* was determined. These regulations were then applied to the default parameter set (Table 1) to understand the impacts of incorrect information on regulation outcome. The bold values represent the optimal outcome for each metric when comparing the objective-meeting HS and MLL.

Life-History Prototypes	Management Objectives	*F*	Regulation (mm)	Harvest (thousands)	Trophy (thousands)	Yield (million kg)	SPR	*J*
LLLP	Compromise	0.8*M*	400-554 HS	**129**	**29.8**	0.14	**0.72**	**0.46**
		0.8*M*	714 MLL	77	13.9	**0.36**	0.71	0.28
	Compromise	2*M*	400-467 HS	**156**	**64.9**	0.14	0.68	**0.46**
		2*M*	800 MLL	68	20.3	**0.37**	**0.72**	0.27
	Trophy	0.8*M*	400-456 HS	**54**	**38.0**	0.04	**0.89**	**0.47**
		0.8*M*	800 MLL	45	20.9	**0.26**	0.83	0.36
	Trophy	2*M*	400-430 HS	**67**	**83.7**	0.05	**0.87**	**0.47**
		2*M*	838 MLL	50	36.6	**0.30**	0.80	0.33
	Harvest	0.8*M*	400-732 HS	**201**	**16.3**	0.32	0.47	**0.38**
		0.8*M*	596 MLL	127	9.3	**0.44**	**0.55**	0.23
	Harvest	2*M*	400-562 HS	**254**	**37.0**	0.27	0.42	**0.44**
		2*M*	750 MLL	94	11.0	**0.44**	**0.62**	0.18
SLHP	Compromise	0.8*M*	200-264 HS	**150**	**61.7**	0.03	**0.78**	**0.36**
		0.8*M*	376 MLL	108	34.8	**0.08**	0.75	0.20
	Compromise	2*M*	200-252 HS	**179**	**121.7**	0.03	**0.76**	**0.36**
		2*M*	404 MLL	113	52.0	**0.09**	0.73	0.15
	Trophy	0.8*M*	200-246 HS	62	**78.9**	0.01	**0.93**	**0.37**
		0.8*M*	418 MLL	**66**	542	**0.06**	0.85	0.27
	Trophy	2*M*	200-242 HS	**82**	**153.9**	0.01	**0.91**	**0.37**
		2*M*	432 MLL	77	96.3	**0.07**	0.82	0.24
	Harvest	0.8*M*	200-362 HS	**230**	**33.3**	0.06	0.56	**0.31**
		0.8*M*	316 MLL	168	21.0	**0.09**	**0.61**	0.16
	Harvest	2*M*	200-268 HS	**266**	**65.8**	0.05	0.53	**0.34**
		2*M*	380 MLL	143	27.3	**0.10**	**0.64**	0.09

SPR = spawning potential ratio, *J* = proportion of fecundity produced by the older half of age classes in the population.

Table S2. Sensitivity test of the performance of harvest slot (HS) and minimum-length limit (MLL) regulations determined with incorrect estimates of the recruitment compensation ratio (*CR*) for two different life-history prototypes (Table 1). The LLLP represents a long-lived low-productive fish population, while the SLHP represents a short-lived high-productive fish population.To determine the best regulation *CR* was increased to 20% greater than the default value (Table 1) and the regulation best meeting each of three management objectives at two fishing mortality levels *F* was determined. These regulations were then applied to the default parameter set (Table 1) to understand the impacts of incorrect information on regulation outcome. The bold values represent the optimal outcome for each metric when comparing the objective-meeting HS and MLL.

Life-History Prototypes	Management Objectives	*F*	Regulation (mm)	Harvest (thousands)	Trophy (thousands)	Yield (million kg)	SPR	*J*
LLLP	Compromise	0.8*M*	400-582 HS	**145**	**27.5**	0.17	0.67	**0.45**
		0.8*M*	720 MLL	74	14.2	**0.35**	**0.71**	0.28
	Compromise	2*M*	400-492 HS	**180**	**59.2**	0.16	0.62	**0.46**
		2*M*	806 MLL	65	22.1	**0.36**	**0.74**	0.28
	Trophy	0.8*M*	400-468 HS	**65**	**36.8**	0.06	**0.87**	**0.47**
		0.8*M*	816 MLL	39	22.9	**0.23**	0.85	0.37
	Trophy	2*M*	400-438 HS	**82**	**81.2**	0.06	**0.84**	**0.47**
		2*M*	850 MLL	45	44.6	**0.28**	0.82	0.35
	Harvest	0.8*M*	400-776 HS	**209**	**13.2**	0.36	0.43	**0.34**
		0.8*M*	574 MLL	137	8.7	**0.45**	**0.53**	0.23
	Harvest	2*M*	400-592 HS	**270**	**30.0**	0.31	0.35	**0.42**
		2*M*	746 MLL	96	10.5	**0.45**	**0.62**	0.18
SLHP	Compromise	0.8*M*	200-274 HS	**168**	**56.1**	0.03	0.74	**0.36**
		0.8*M*	378 MLL	107	35.3	**0.08**	**0.75**	0.20
	Compromise	2*M*	200-254 HS	**198**	**114.2**	0.03	0.73	**0.36**
		2*M*	410 MLL	105	61.4	**0.09**	**0.75**	0.17
	Trophy	0.8*M*	200-248 HS	**73**	**77.1**	0.01	**0.91**	**0.37**
		0.8*M*	426 MLL	58	58.7	**0.06**	0.87	0.28
	Trophy	2*M*	200-242 HS	**82**	**153.9**	0.01	**0.91**	**0.37**
		2*M*	442 MLL	64	110.7	**0.06**	0.86	0.27
	Harvest	0.8*M*	200-390 HS	**237**	**26.1**	0.07	0.52	**0.27**
		0.8*M*	302 MLL	179	19.8	**0.10**	**0.58**	0.16
	Harvest	2*M*	200-282 HS	**269**	**51.3**	0.05	0.47	**0.33**
		2*M*	380 MLL	143	27.3	**0.10**	**0.64**	0.09

M = instantaneous annual natural mortality rate, SPR = spawning potential ratio, *J* = proportion of fecundity produced by the older half of age classes in the population.

Table S3. Sensitivity test of the performance of harvest slot (HS) and minimum-length limit (MLL) regulations determined with incorrect estimates of the instantaneous fisheries exploitation rate (F) for two different life-history prototypes (Table 1). The LLLP represents a long-lived low-productive fish population, while the SLHP represents a short-lived high-productive fish population.To determine the best regulation F was decreased to 20% below the default value (Table 1) and the regulation best meeting each of three management objectives at two fishing mortality levels F was determined. These regulations were then applied to the default parameter set (Table 1) to understand the impacts of incorrect information on regulation outcome. The bold values represent the optimal outcome for each metric when comparing the objective-meeting HS and MLL.

Life-History Prototypes	Management Objectives	F	Regulation (mm)	Harvest (thousands)	Trophy (thousands)	Yield (million kg)	SPR	J
LLLP	Compromise	0.8M	400-606 HS	**158**	**25.6**	0.20	0.63	**0.45**
		0.8M	692 MLL	86	12.8	**0.38**	**0.68**	0.27
	Compromise	2M	400-506 HS	**200**	**54.1**	0.19	0.57	**0.46**
		2M	790 MLL	73	17.9	**0.38**	**0.71**	0.25
	Trophy	0.8M	400-476 HS	**72**	**36.2**	0.06	**0.85**	**0.47**
		0.8M	806 MLL	43	21.6	**0.25**	0.83	0.36
	Trophy	2M	400-444 HS	**97**	**78.4**	0.08	0.81	**0.47**
		2M	844 MLL	47	41.1	**0.29**	**0.81**	0.35
	Harvest	0.8M	400-822 HS	**215**	**10.2**	0.39	0.40	**0.29**
		0.8M	516 MLL	164	7.5	**0.46**	**0.47**	0.22
	Harvest	2M	400-628 HS	**282**	**22.4**	0.34	0.29	**0.39**
		2M	718 MLL	112	7.9	**0.48**	**0.56**	0.14
SLHP	Compromise	0.8M	200-308 HS	**183**	**53.0**	0.04	0.71	**0.36**
		0.8M	368 MLL	115	32.6	**0.08**	**0.73**	0.19
	Compromise	2M	200-256 HS	**214**	**106.9**	0.04	0.69	**0.36**
		2M	408 MLL	108	56.7	**0.09**	**0.74**	0.16
	Trophy	0.8M	200-250 HS	**84**	**75.2**	0.01	**0.90**	**0.37**
		0.8M	422 MLL	62	56.7	**0.06**	0.86	0.27
	Trophy	2M	200-244 HS	**100**	**149.9**	0.02	**0.88**	**0.37**
		2M	442 MLL	64	110.7	**0.06**	0.86	0.27
	Harvest	0.8M	200-410 HS	**238**	**20.2**	0.07	0.48	**0.24**
		0.8M	262 MLL	196	16.7	**0.09**	**0.54**	0.15
	Harvest	2M	200-318 HS	**267**	**40.4**	0.05	0.42	**0.31**
		2M	370 MLL	155	22.3	**0.11**	**0.60**	0.08

M = instantaneous annual natural mortality rate, SPR = spawning potential ratio, J = proportion of fecundity produced by the older half of age classes in the population.

Table S4. Sensitivity test of the performance of harvest slot (HS) and minimum-length limit (MLL) regulations determined with incorrect estimates of the length at maturations (L_{mat}) for two different life-history prototypes (Table 1). The LLLP represents a long-lived low-productive fish population, while the SLHP represents a short-lived high-productive fish population.To determine the best regulation L_{mat} was decreased to 20% below the default value (Table 1) and the regulation best meeting each of three management objectives at two fishing mortality levels F was determined. These regulations were then applied to the default parameter set (Table 1) to understand the impacts of incorrect information on regulation outcome. The bold values represent the optimal outcome for each metric when comparing the objective-meeting HS and MLL.

Life-History Prototypes	Management Objectives	F	Regulation (mm)	Harvest (thousands)	Trophy (thousands)	Yield (million kg)	SPR	J
LLLP	Compromise	0.8M	360-516 HS	**175**	**27.7**	0.13	0.66	**0.46**
		0.8M	698 MLL	83	13.1	**0.37**	**0.68**	0.27
	Compromise	2M	360-412 HS	**215**	**60.0**	0.11	0.63	**0.47**
		2M	796 MLL	70	19.4	**0.37**	**0.72**	0.26
	Trophy	0.8M	360-390 HS	**77**	**37.1**	0.04	**0.87**	**0.47**
		0.8M	800 MLL	45	20.9	**0.26**	0.83	0.36
	Trophy	2M	360-348 HS	**98**	**81.0**	0.04	**0.84**	**0.47**
		2M	842 MLL	48	39.2	**0.29**	0.81	0.34
	Harvest	0.8M	360-736 HS	**253**	**13.4**	0.31	0.40	**0.38**
		0.8M	542 MLL	152	8.0	**0.45**	**0.49**	0.23
	Harvest	2M	360-526 HS	**327**	**30.6**	0.23	0.34	**0.45**
		2M	736 MLL	102	9.5	**0.46**	**0.60**	0.16
SLHP	Compromise	0.8M	160-266 HS	**167**	**57.6**	0.03	0.75	**0.36**
		0.8M	380 MLL	104	36.1	**0.08**	**0.76**	0.21
	Compromise	2M	160-252 HS	**202**	**111.8**	0.03	0.72	**0.36**
		2M	410 MLL	105	61.4	**0.09**	**0.75**	0.17
	Trophy	0.8M	160-246 HS	**76**	**76.4**	0.01	**0.91**	**0.37**
		0.8M	426 MLL	58	58.7	**0.06**	0.87	0.28
	Trophy	2M	160-238 HS	**80**	**150.4**	0.01	**0.90**	**0.37**
		2M	444 MLL	62	113.3	**0.06**	0.86	0.27
	Harvest	0.8M	160-380 HS	**240**	**27.5**	0.06	0.52	**0.29**
		0.8M	308 MLL	176	20.1	**0.09**	**0.59**	0.16
	Harvest	2M	160-268 HS	**275**	**56.4**	0.05	0.49	**0.34**
		2M	382 MLL	141	28.1	**0.10**	**0.65**	0.10

M = instantaneous annual natural mortality rate, SPR = spawning potential ratio, J = proportion of fecundity produced by the older half of age classes in the population.